Universitat Autònoma de Barcelona

Bone-Cracking Hyenas (Carnivora, Hyaenidae) from the European Neogene and Quaternary: Taxonomy, Paleobiology and Evolution

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Doctoral dissertation

Víctor Vinuesa

Thesis advisors:
Joan Madurell-Malapeira
David M. Alba

Thesis tutor:
Ricard Martínez

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Cover image: Spotted hyena drinking in a small lake

(modified from a photo of Israel M. Sánchez)

Back cover: Rendering of a skull 3D model of *Crocuta ultima*

Departament de Geologia, Facultat de Ciències,
Universitat Autònoma de Barcelona

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Víctor Vinuesa

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Dissertation by Víctor Vinuesa Vinuesa to obtain the Doctor's degree in Geology

Thesis Advisors:

Dr. Joan Madurell-Malapeira, Institut Català de Paleontologia

Dr. David M. Alba, Institut Català de Paleontologia

Thesis Tutor:

Dr. Ricard Martínez, Universitat Autònoma de Barcelona

Joan Madurell-Malapeira

David M. Alba

Víctor Vinuesa

Abstract

The family Hyaenidae (Mammalia, Carnivora) include four extant species restricted to Africa and Asia: the bone-cracking hyenas (*Crocuta crocuta*, *Hyaena hyaena*, *Parahyaena brunnea*) and the myrmecophagous aardwolf (*Proteles cristata*). During the Neogene and Quaternary, hyaenids were more diverse and widely distributed throughout the Old World and even North America, although their diversity and ecomorphological disparity progressively declined since the late Miocene onwards. Many controversies remain about the origin and diversification of hyaenids. This dissertation aims to address some of these topics based on new remains and innovative techniques. It includes a compendium of published articles, organized in two blocks: the first consists of five papers about extinct hyaenids (*Hyaenictis*, *Pliocrocuta* and *Pachycrocuta*), mostly devoted to the morphological description and morphometric comparison of previously unpublished fossils and related taxonomic issues, with emphasis on dental adaptations to durophagy; the second block relies on 3D imaging techniques applied to computed tomography (CT) scans to study the internal cranial anatomy of extinct hyaenids (*Pliocrocuta*, *Crocuta*), with emphasis on brain morphology and proportions to derive paleoneurological inferences on social behavior. The main conclusions of the dissertation may be grouped as follows:

1. Taxonomy: The unpublished material from Ronda Oest de Sabadell (late Miocene), Villarroya and La Puebla de Valverde (Late Pliocene-Early Pleistocene), and Cueva Victoria (Late Early Pleistocene) is attributed, respectively, to *Hyaenictis* aff. *almerai*, *Pliocrocuta perrieri*, and *Pachycrocuta brevirostris*. The authorship of the latter is corrected from "Aymard, 1846" to "Gervais, 1850". Differences in brain morphology support the distinction of both *Crocuta spelaea* and *Crocuta ultima* from *Crocuta crocuta* at the species rank.
2. Paleobiology: The taphonomic study of the large herbivore remains from the Vallparadís Section (Late Early Pleistocene) indicates that *Pachycrocuta brevirostris* was the main bone modificator agent in the site. In turn, the developed frontal sinuses of *Pliocrocuta perrieri*, related to improved skull resistance against bite stresses, support a durophagous diet for this species, and the same holds for the zig-zag enamel microstructural pattern of both *Pliocrocuta perrieri* and *Hyaenictis* aff. *almerai*, which enable to reassign the latter to the transitional bone-cracking ecomorphotype 5. With regard to brain morphology, *Pliocrocuta perrieri*, *Crocuta spelaea* and *Crocuta ultima* resemble extant hyaenines, although their frontal lobe is less developed than in *Crocuta crocuta*, suggesting a less complex social behavior than in the latter species (comparable to that of *Hyaena* and *Parahyaena*). Currently available paleoneurological evidence indicates that the hyaenid brain evolved towards greater relative size and complexity throughout the Miocene and that *Proteles* probably displays the most plesiomorphic brain among extant hyaenids.
3. Evolutionary history: Based on the new morphofunctional and paleoneurological evidence presented, new hypotheses for the evolution of bone-cracking hyaenids are proposed, such as the origin of hyaenines from *Hyaenictis*. Some of these hypotheses differ from those supported by morphology-based cladistic analyses but are in greater agreement with molecular evidence. The results highlight the potential of cranial internal morphology as a source of phylogenetically informative data that, in the future, might hopefully enable more comprehensive and better resolved phylogenetic analyses that could settle some of the current debates about the evolutionary history of hyaenids.

Resumen

La familia Hyaenidae (Mammalia, Carnivora) incluye actualmente cuatro especies, que están restringidas a África y Asia: las hienas rompedoras de huesos (*Crocuta crocuta*, *Hyaena hyaena*, *Parahyaena brunnea*) y el mirmecófago lobo de tierra (*Proteles cristata*). Durante el Neógeno y el Cuaternario, las hienas tenían mayor diversidad y se distribuían ampliamente por todo el Viejo Mundo y parte de Norteamérica, aunque su diversidad y disparidad ecomorfológica fueron disminuyendo progresivamente desde finales del Mioceno. El origen y diversificación de los hiénidos sigue siendo objeto de controversias. Esta tesis tiene como objetivo abordar algunas de estas problemáticas mediante el estudio de nuevos restos y el uso de técnicas innovadoras. Esta tesis está formada por un compendio de artículos, organizados en dos bloques: el primero consta de cinco publicaciones sobre hiénidos extintos (*Hyaenictis*, *Pliocrocuta* y *Pachycrocuta*), principalmente dedicadas a la descripción y comparación morfométrica de fósiles inéditos y sus problemas taxonómicos, con énfasis en las adaptaciones dentales a la durofagia; el segundo bloque se centra en el estudio de la anatomía craneal interna de los hiénidos extintos (*Pliocrocuta*, *Crocuta*), obtenida mediante técnicas de visualización aplicadas a escáneres de tomografía computarizada (CT), con especial énfasis en la morfología cerebral y sus proporciones, en base a las cuales se pueden realizar inferencias paleobiológicas sobre el comportamiento social de cada especie. Las conclusiones principales de la tesis se pueden agrupar de la siguiente manera:

1. Taxonomía: el material inédito de Ronda Oest de Sabadell (Mioceno superior), Villarroya y La Puebla de Valverde (Plioceno Superior-Pleistoceno Inferior) y Cueva Victoria (Pleistoceno Inferior tardío) se atribuye, respectivamente, a *Hyaenictis* aff. *almerai*, *Pliocrocuta perrieri* y *Pachycrocuta brevirostris*. La autoría de este último se corrige de "Aymard, 1846" a "Gervais, 1850". Diferencias en la morfología cerebral, tanto en *Crocuta spelaea* como en *Crocuta ultima*, con respecto a *Crocuta crocuta* apoyan su distinción con rango de especie.
2. Paleobiología: El estudio tafonómico de los grandes restos de herbívoros de la Sección de Vallparadís (Pleistoceno Inferior tardío) indica que *Pachycrocuta brevirostris* fue el principal agente modificador de huesos en el yacimiento. A su vez, los senos frontales desarrollados de *Pliocrocuta perrieri*, relacionados con la resistencia mejorada del cráneo durante las tensiones en la mordida, respaldan una dieta durófaga para esta especie. Esto se aplica también al patrón microestructural en zig-zag del esmalte de *Pliocrocuta perrieri* y *Hyaenictis* aff. *almerai*, que permite reasignar esta última al ecomorfotipo 5 (hienas rompedoras de huesos transicionales). La morfología cerebral de *Pliocrocuta perrieri*, *Crocuta spelaea* y *Crocuta ultima* se parece a la de las hienas actuales, aunque su lóbulo frontal está menos desarrollado que en *Crocuta crocuta*, lo que sugiere una menor complejidad del comportamiento social que la presente en esta última (comparable a las de *Hyaena* y *Parahyaena*). Los datos paleoneurológicos disponibles indican que el cerebro de los hiénidos evolucionó hacia una mayor complejidad y tamaño a lo largo del Mioceno y que *Proteles* presenta, probablemente, el cerebro más plesiomórfico entre hiénidos actuales.
3. Historia evolutiva: En base los nuevos datos morfofuncionales y paleoneurológicos presentados, se proponen nuevas hipótesis para la evolución de las hienas rompedoras de huesos, como el origen de los hyaeninos actuales a partir de *Hyaenictis*. Algunas de estas hipótesis difieren de los análisis cladísticos basados en morfología, pero están en mayor concordancia con los datos moleculares. Los resultados destacan el potencial del estudio de la morfología interna del craneo como posible fuente de datos filogenéticamente informativos que, en el futuro, podrían permitir un análisis filogenético más completos y más bien resueltos que podría zanjar algunos de los debates actuales sobre la historia evolutiva de los hiénidos.

Contents

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Aims and structure of this work

The main objective of this doctoral dissertation is focused on the origin and evolution of bone-cracking hyenas in Eurasia. It also aims to exemplify the usefulness of innovative methods to investigate the phylogeny and paleobiology of extinct hyaenids. The evolutionary history of hyaenids is critically revisited in the light of the new data provided on the taxonomy, and paleobiology of various bone-cracking fossil hyenas. The combination of digital techniques (for retrieving internal anatomical data) with classical methods applied to the study of fossils remains enables a better understanding of the paleobiology of extinct taxa. This information sheds new light on the evolutionary history of bone-cracking hyenas, by supporting or questioning previous hypotheses on the adaptations and phylogeny of the group, as well as by leading to the proposal of new hypotheses to be tested in the future. The dissertation emphasizes the usefulness of CT scans for acquiring inner cranial data to investigate brain morphology (with implications for paleobiological inferences about social behavior), as well as to investigate other characters that may contribute to phylogenetic analyses of the group in order to resolve phylogenies combining extinct and extant taxa.

This dissertation is divided into several chapters that can be grouped into various parts. The first part of the dissertation introduces the main topics and the methodology used (chapters 1–3). In particular, the Introduction provides a summary of both extant and extinct hyaenids, focusing in their biology and evolutionary history (chapter 1) and of the geological background of the eight sites from where the studied material comes from (chapter 2). Chapter 3 is the materials and methods section, which reports on the studied and comparative samples, the measurements and anatomical nomenclature employed, and CT scanning details. The second part of the dissertation includes the results (chapters 4–10), consisting of a set of published articles that are organized in two main blocks (see below). The third part of the dissertation follows, being focused on the discussion of the results (chapter 11) as well as the main conclusions (chapter 12). Finally, the fourth part of the dissertation includes the references for the first and third parts of the dissertation (i.e., except those included in the published papers) and the appendix (with relevant accessory data concerning *Adcrocuta eximia*).

The second part of the dissertation constitutes the main body of this work and includes up to seven published papers, each one corresponding to a different chapter. They are organized in two different blocks. The first one (chapters 4–8) is devoted to fossil bone-cracking hyenas in a rather classical way, by relying on external craniodental features to better characterize the taxonomy and paleobiology the studied genera. In particular, these chapters are focused on the description and comparisons of new material belonging to well-known bone-cracking hyaenid genera (*Pliocrocuta* and *Pachycrocuta*), as well as the poorly known genus *Hyaenictis*. Two additional chapters related to *Pachycrocuta* are included in the first block of published papers: one focusing on the bone-cracking habits of *Pachycrocuta*, and another one about nomenclatural issues. The second set of papers (chapters 9 and 10) are mostly devoted to the paleobiology of some bone-craking hyaenids by taking a paleoneurological approach that essentially relies on CT imaging techniques. In particular, these chapters include the description of the brain endocasts of three different bone-cracking haenas (*Crocuta spelaea*, *Crocuta ultima* and *Pliocrocuta perrieri*), as well as their comparison with extant representatives of the family, in order to make paleobiological inferences on social behavior.

The Discussion (chapter 11) pivots around four main topics: the new contributions to the paleobiology and evolution of bone-cracking hyenas; the evolution of durophagy in relation to craniodental adaptations; paleoneurology and brain evolution in bone-cracking hyenas; and an overview of the evolutionary history of the family Hyaenidae by incorporating the new results reported in this dissertation. The short Conclusions (chapter 12) summarize the evidence put forward in the previous chapters.

Chapter 1. Introduction

1.1. Extant hyaenids

Extant hyenas are included in the family Hyaenidae Gray, 1821 (hyaenids) within the order Carnivora Bowdich, 1821 (carnivorans). There are four extant species distributed in Africa and Asia: the spotted hyena, *Crocuta crocuta* Erxleben, 1777; the striped hyena, *Hyaena hyaena* Linnaeus, 1758; the brown hyena, *Parahyaena brunnea* Thunberg, 1820; and the aardwolf, *Proteles cristata* Sparrman, 1783. Although hyaenids are commonly known as medium to large dog-like species that eat only carrion, this is only partially true for two of the living species. The spotted hyena is an active hunter, being even more successful in that task than lions (Kruuk, 1972a). In turn, the aardwolf is a relatively small (10 kg) insectivore that eats mainly termites. Hyenas are also popularly renowned for their laugh, despite the fact that these particular noises ('whoops') are only made by the highly social spotted hyena (Kruuk, 1972a, 1976; Mills, 1990). This call is used mainly for communication (in which the common 'laugh' is fear) between clan members within the hierarchized, large and complex groups (with up to 90 members) of this species. A highly developed sociability is not characteristic of hyaenids as a whole since the other three species are less gregarious, even solitary. Despite differences in diet and behavior, all four species of extant hyaenids share some important morphological differences that readily distinguish them from other Feliformia Kretzoi, 1945 (as they are more closely related to cats than to dogs), such as Felidae, Herpestidae, and Viverridae. These synapomorphies of extant hyaenids include the following features (Werdelin and Solounias, 1991): the lack of baculum, the morphology of the deciduous dentition, the lack of alisphenoid canal in the sphenoid bone, the divided auditorial bullae, the proximity of the paraoccipital processes to the bullae (as the latter are expanded), the posteriorly expanded ectotympanic bone, and the caudally reduced endotympanic bone.

1.1.1. Systematics

Class MAMMALIA Linnaeus, 1758
Order CARNIVORA Bowdich, 1821
Suborder FELIFORMIA Kretzoi, 1945
Family HYAENIDAE Gray, 1821
Subfamily HYAENINAE Gray, 1821
Genus *Crocuta* Kaup, 1828
Crocuta crocuta (Erxleben, 1777)

Spotted hyena

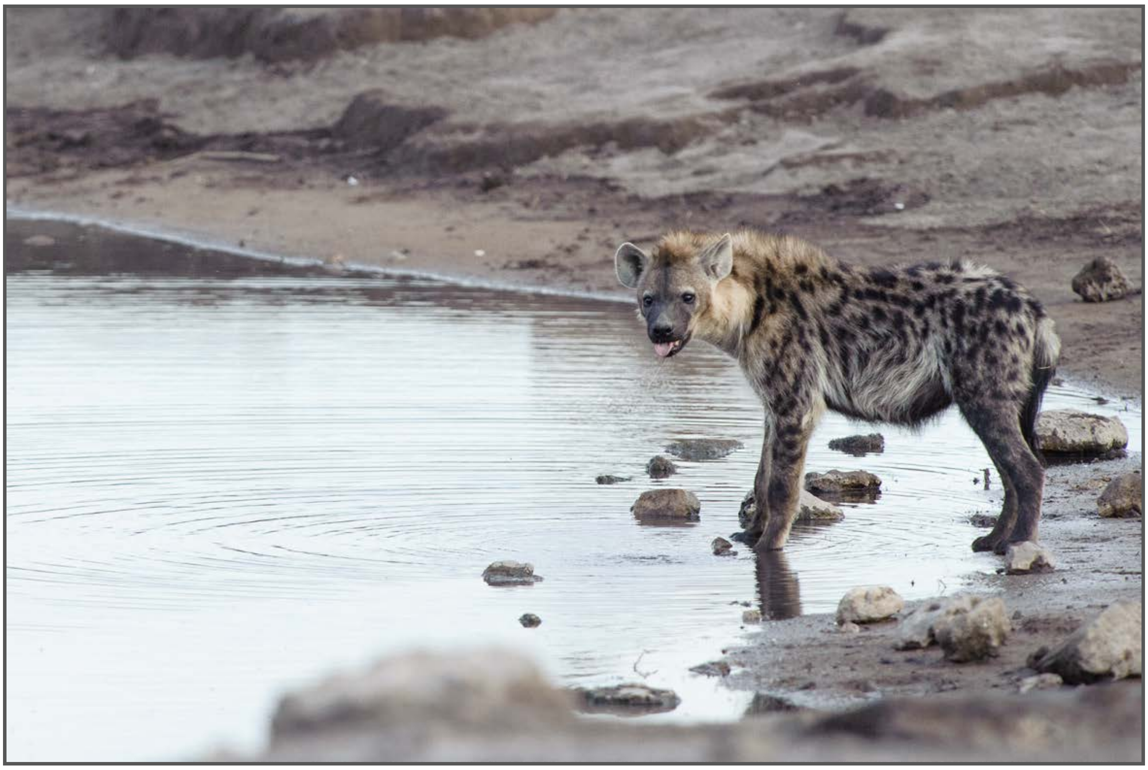

Figure 1.1: The spotted hyena, *Crocuta crocuta* (Photo by Israel M. Sánchez).

The spotted hyena (*Crocuta crocuta*, Fig. 1.1) is the largest of the extant hyaenids, with a body length of 125–160 cm, a height at the shoulder of 77–80 cm, and a body mass of 45–85 kg. Females are approximately 10% larger than males, although such differences vary locally, being more marked in South African populations. The head is large and rounded, the muzzle is short, the muscles are well-developed on the cheek and, unlike in other extant hyaenids, the ears are rounded. The fur is short and sandy, light brown or even reddish-brown in coloration, with dark dots around the whole body. The back is sloping due to the longer forelimbs. The tail is short and ends in a bushy and black tip with long hair. Like in other extant hyaenids, there is a well-developed anal gland below the tail. The paws have only 4 toes. Females have an enlarged clitoris, which looks like a male penis, which hinders sex identification (although they can be sexed based on several minor differences between males and females, such as the belly shape or the anal glands; Holekamp and Kolowski, 2009; Kingdon and Hoffmann, 2013). This hyena is the only living species within the genus *Crocuta.* Although it was primarily described as *Canis crocuta* Erxleben, 1777, it was eventually transferred to *Hyaena* (Thunberg, 1811), and finally, its own genus was created shortly thereafter (Kaup, 1828).

Genus *Hyaena* Brisson, 1762

Hyaena hyaena (Linnaeus, 1758)

Striped hyena

Figure 1.2: The striped hyena, *Hyaena hyaena* (Photo by Valerie, 2011, CC BY-NC-ND 2.0, Flickr.com).

The striped hyena (*Hyaena hyaena*, Fig. 1.2) is the smallest hyaenine, with a body length of 110–115 cm, a shoulder height of 66–75 cm, and a body mass of 26–41 kg. Like the spotted hyena, this species was described as *Canis hyaena* Linnaeus, 1758 at the beginning, but transferred to a new genus, *Hyaena*, shortly thereafter (Brünnich, 1777). Some researchers distinguish up to five subspecies based on differences in size and pelage (Holekamp and

Kolowski, 2009): *H. h. hyaena* Linnaeus, 1758, from India; *H. h. syriaca* Matschie, 1900, from Syria and Israel; *H. h. sultana* Pocock, 1934, from the Arabian Peninsula; *H. h. barbara* de Blainville, 1844; from the northwest of Africa; and *H. h. dubbah* Meyer, 1793, from the northeast of Africa. Some population display sexual dimorphism (e.g., *H. h. syriaca*). The head and neck are massive, as in spotted and brown hyenas, and the back similarly slopes due to the longer forelimbs than hind limbs. The fur is long with a shaggy appearance, and light-gray in color, with vertical black stripes along the body, and horizontal stripes on the legs. The muzzle is black and there are two stripes on the cheek. The ears are pointy. The mane is light gray colored, runs along the whole length of the back, and displays longer hair than other areas of the body, being erected to make body size appear larger. The tail is long, bushy, and black and gray in coloration. Northern subspecies are slightly larger than southern ones. They do not vary much in color, although there are some minor differences (e.g., *H. h. sultana* displays yellow marks under the eyes and a dorsal crest with a mix of black and gray colors) (Holekamp and Kolowski, 2009; Kingdon and Hoffmann, 2013).

Genus *Parahyaena* Hendey, 1974
Parahyaena brunnea (Thunberg, 1820)

Brown hyena

The brown hyena (*Parahyaena brunnea*, Fig. 1.3) is the second largest extant hyaenid (Holekamp and Kolowski, 2009), with a body length of 110–140 cm, a shoulder height of 80 cm, and a body mass that varies regionally from 28 to 48 kg (about 40 kg on average). It displays minor sexual dimorphism, being the males slightly larger than females. The head is broad, with a short muzzle, pointy ears, a thick neck, a backwards-sloping back with longer hair than the rest of the body, longer and stronger forelimbs compared to the hind limbs, and a short tail with long hair. The fur is shaggy and dark brown in color, and it can get erected when necessary. The legs are banded with light and dark horizontal stripes (Holekamp and Kolowski, 2009; Kingdon and Hoffmann, 2013). Like the spotted hyena, this is the only living species included within the genus. It was initially classified in *Hyaena* (Thunberg, 1820), and for a long time it was included within that genus, but eventually a new subgenus, *Parahyaena*, was erected for it by Hendey, 1974, being subsequently elevated to genus rank (Werdelin and Solounias, 1991); some authors, however, still refer to it as *Hyaena brunnea.*

Figure 1.3: The brown hyena, *Parahyaena brunnea* (photo taken from Pixabay.com, CC0 Creative commons).

Subfamily PROTELINAE Geoffroy Saint-Hilaire, 1851

Genus *Proteles* Geoffroy Saint-Hilaire, 1824

Proteles cristata (Sparrman, 1783)

Aardwolf

The aardwolf (*Proteles cristata*, Fig. 1.4) is the smallest of extant hyaenids, with a body length of 55–80 cm, a height of 45–50 cm, a tail length of 20–30 cm, and an average body mass of 10 kg with seasonal fluctuations (Holekamp and Kolowski, 2009). This species was initially classified in the genus *Viverra* (Sparrman, 1783), but in the 19th century, Geoffroy Saint Hilaire (1824) erected a genus for it. Its position within Feliformia was unclear until its inclusion within Hyaenidae through karyotypic analysis (Wurster and Bernirschke, 1968). Two subspecies are recognized (Holekamp and Kolowski, 2009): *Proteles cristata cristata* Sparrman, 1782, from East Africa; and *Proteles cristata septentrionalis* Rothschild, 1902, from South Africa. This species displays dark vertical stripes on a buff yellowish-white or rufous body, also with irregular horizontal black lines on the legs, and a bushy tail blackened in the end. The fur is 2 cm long, with longer parts along the mane and in the tail. The mane itself is erectile and extends along the whole body-length. The neck is long with a pale gray-white coloring. The legs

Figure 1.4: The aardwolf, *Proteles cristata* (Photo by Valerie, 2014, CC BY-NC-ND 2.0, Flickr.com).

are long and slender, and end in black paws. The forelegs are slightly longer than the hind legs, resulting in the characteristic slope in the back of all hyaenids. There is no clear sexual dimorphism (Holekamp and Kolowski, 2009). In the head, the ears are pointy, and the muzzle is black. This species displays a series of unique adaptations among hyaenids for feeding on termites: long and spatulate tongue, with large and varied papillae, and large submaxillary glands that generate abundant sticky saliva. The cheek teeth are highly reduced, thin and unicuspid, but the canines remain large and sharp, to be used in territorial disputes. Finally, the tympanic bullae are extraordinarily enlarged (Holekamp and Kolowski, 2009; Kingdon and Hoffmann, 2013).

1.1.2. Phylogeny

Several works have dealt with the phylogenetic relationships of the Hyaenidae and their position within the Feliformia. With regard to the living species, Gaudry (1862-1867) first proposed that *Hyaena hyaena* and *Parahyaena brunnea* were more closely related to each other than to *Crocuta crocuta*. In contrast, Schlosser (1890) proposed that *Parahyaena brunnea* was more closely related to *Crocuta crocuta* than to *Hyaena hyaena*, because *Parahyaena brunnea* and *Crocuta crocuta* share more traits in common. While the former hypothesis was subsequently followed by many authors (Pilgrim, 1932; Ewer, 1955; Thenius, 1966; Hendey, 1974), the latter was supported by two more recent phylogenetic analyses (Galiano and Frailey, 1977; Werdelin and Solounias, 1991). In particular, Werdelin and Solounias (1991) addressed this topic from a paleontological and morphological perspective, and their phylogeny was the first to include *Proteles*. The lack in *Proteles* of many of the dental characters of phylogenetic value among hyaenids, caused by the highly reduced dentition of the former, led these authors to perform two different analyses: including *Proteles* with ordered characters; and without *Proteles* (being considered as a basal form a posteriori). The latter analysis recovered *Parahyaena* and *Crocuta* as sister taxa, whereas the inclusion of *Proteles* in the former analysis placed it as the sister group of the remaining extant hyaenids, but did not resolve whether *Crocuta* is the sister taxon of *Hyaena* or *Parahyaena*. Whereas karyotypic analyses (Wurster and Benirschke, 1968) had already supported the inclusion of *Proteles* within the Hyaenidae (because all four extant species share an almost identical karyotype), it was not until subsequent analyses of mitochondrial DNA (Jenks and Werdelin, 1998; Koepfli et al., 2006) that the basal-most position *Proteles* among the hyaenids was confirmed, with *Hyaena* and *Parahyaena* emerging as sister taxa, more closely related to one another than to *Crocuta.*

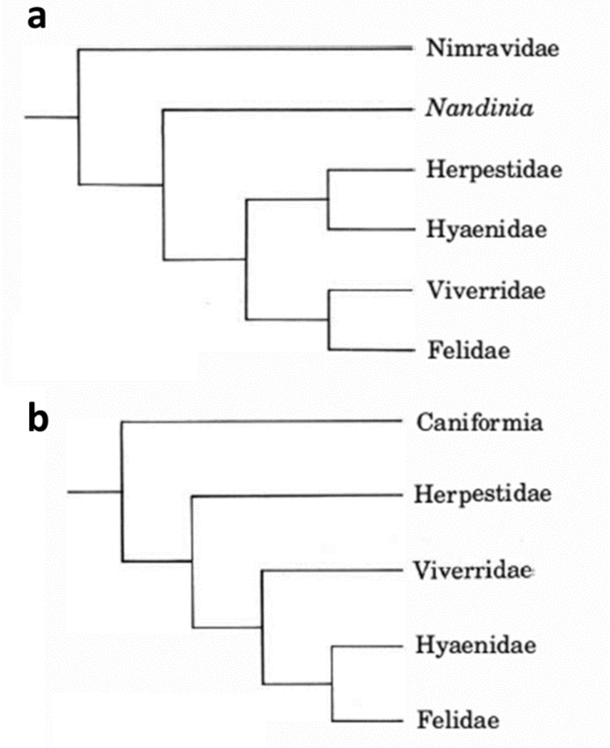

Figure 1.5: Phylogenetic position of the Hyaenidae within the Feliformia according to previous authors: a, Hunt (1987); b, Wozencraft (1989). Modified from Werdelin and Solounias (1991).

With regard to the systematic position of Hyaenidae as a whole, their phylogenetic relationships with other Feliformia were intensely debated during the 1980s and 1990s (Flynn and Galiano 1982; Flynn et al., 1988; Hunt 1987, 1989; Wozencraft, 1989; Fig. 1.5). Two hypotheses were proposed: Hyaenidae and Herpestidae as sister taxa (Hunt, 1987, 1989; Veron, 1995); and Hyaenidae and Felidae as sister taxa (Wozencraft, 1989, 1993; Wyss and Flynn, 1993; Bininda-Emons et al., 1999). An alternative hypothesis of Hyaenidae and Viverridae as sister taxa was discounted by DNA-DNA hybridization analyses (Wayne et al., 1989). Subsequently, mitochondrial DNA analyses confirmed the first hypothesis above, i.e., that herpestids are the extant sister taxon of hyaenids (Flynn and Nedbal, 1998; Gaubert and Veron, 2003; Yoder et al., 2003; Yu et al., 2004; Koepfli et al., 2006). More recent molecular analyses have further clarified the divergence time between the various feliform and hyaenid lineages (Fig. 1.6; Koepfli et al., 2006): ca. 36.2 from Felidae, 35.2 Ma from Viverridae, and 29.2 Ma from Herpestidae; in turn, the bone-cracking clade would have diverged from the *Proteles* lineage ca. 10.6 Ma, *Crocuta* from the both *Hyaena*+*Parahyaena* clade ca. 8.6 Ma, and the two latter genera would have diverged from one another 4.2 Ma. Overall, molecular analyses have shown that the Hyaenidae are most closely related to the Herpestidae (with the Viverridae being polyphyletic) and that *Hyaena* and *Parahyaena* are more closely related to each other than to *Crocuta*, with *Proteles* being the basal-most extant hyaenid.

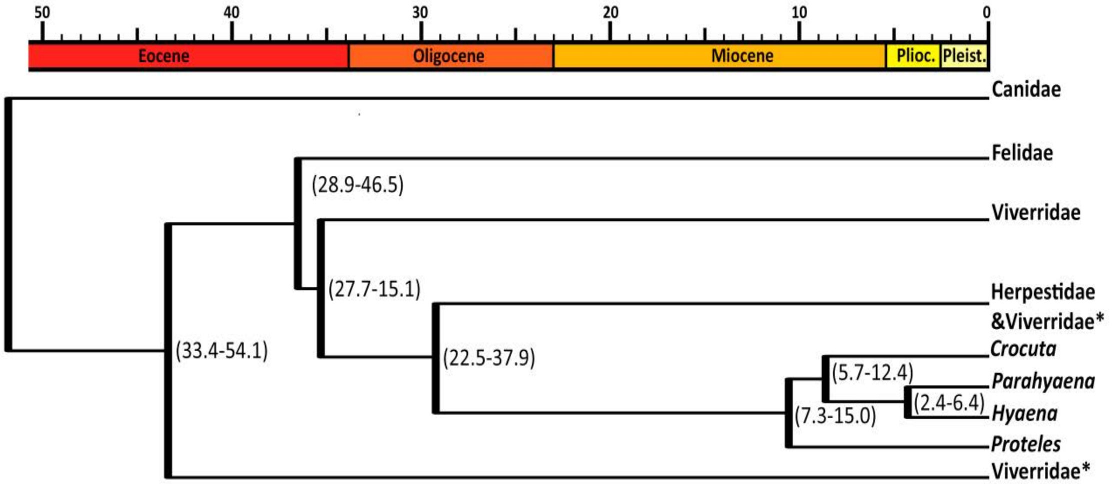

Figure 1.6: Current phylogeny of the extant Hyaenidae with divergence ages (in Ma) for each node (data taken from Koepfli et. al., 2006). The asterisks denote that the Viverridae are polyphyletic according to Koepfli et al. (2006). The two species excluded from the main group of Viverridae are: *Nandinia binotata* Pocock, 1929, placed as sister taxon of the remaining Feliformia; and *Cryptoprocta ferox* Bennet, 1833, placed close to the Herpestidae.

1.1.3. Anatomy

Skeleton

Skull and dentition. The skull of hyaenids is composed of several bones fused together to compose the cranium, as well as an independent but articulated bone, the mandible, which overall have masticatory, respiratory and sensory functions (Fig. 1.7). The splanchnocranium is the most anterior part of the cranium, being formed by several paired bones (maxillae, premaxillae, palatines, lacrimals, nasals, zygomatics) and the single vomer. This region hosts respiratory, olfactory and masticatory functions. Hyaenids lack an alisphenoid canal, which in other carnivorans is placed within the orbit. The posterior half of the cranium is the neurocranium (or braincase), which mainly protects the brain, and is formed by the frontals (partially), parietals, temporals, and occipitals. The basicranium, in turn, is formed by the basisphenoid, the pterygoid, the occipital, and the tympanic portion of the temporal. In hyaenids, the latter is characterized by an inflated tympanic bulla. The mandible is formed exclusively by the dentaries, which hold the lower dentition. The right and left hemimandibles are not fused at the mandibular symphysis.

Extant hyenas display two different skull morphotypes: one adapted for durophagy (the ability to consume hard food items) and another one adapted for myrmecophagy (termite consumption). The durophagous skull (Fig. 1.8), displayed by *Crocuta*, *Hyaena* and *Parahyaena*, is characterized by a series of features that provide with an enhanced ability for breaking bones. In particular, the zygomatic arches are broad and swing out at the back, which coupled with the high sagittal crest enables the presence of large masseter and temporalis muscles. These two features are more developed in the spotted hyena than in the other two bone-crackers, the stripped and brown hyenas. Moreover, the muzzle is generally shorter than in canids, but wider (especially at the palate). As a result, together with the height and curvature of the sagittal crest, the skull of these taxa displays a convex profile in lateral view. The distal elongation of the frontal sinuses, which completely overlap the brain, is also characteristic. Due to this configuration, the sagittal crest is triangular in coronal view (instead of being a flat bony wall), which provides with a greater resistance against bite stresses (Paulli, 1900; Joeckel, 1998; Tanner et al., 2008). In turn, the mandibular corpus is deep and robust, with a convex basal margin. The mandible also displays a wide and deep masseteric fossa, in accordance with the above-mentioned features of the skull. Finally, the coronoid process is high. In general terms, the dentition of bone-cracking hyaenids is similar to that of felids, although the teeth are overall wider and stouter (Fig 1.8a-c). The molars, except for the first lower molar, are

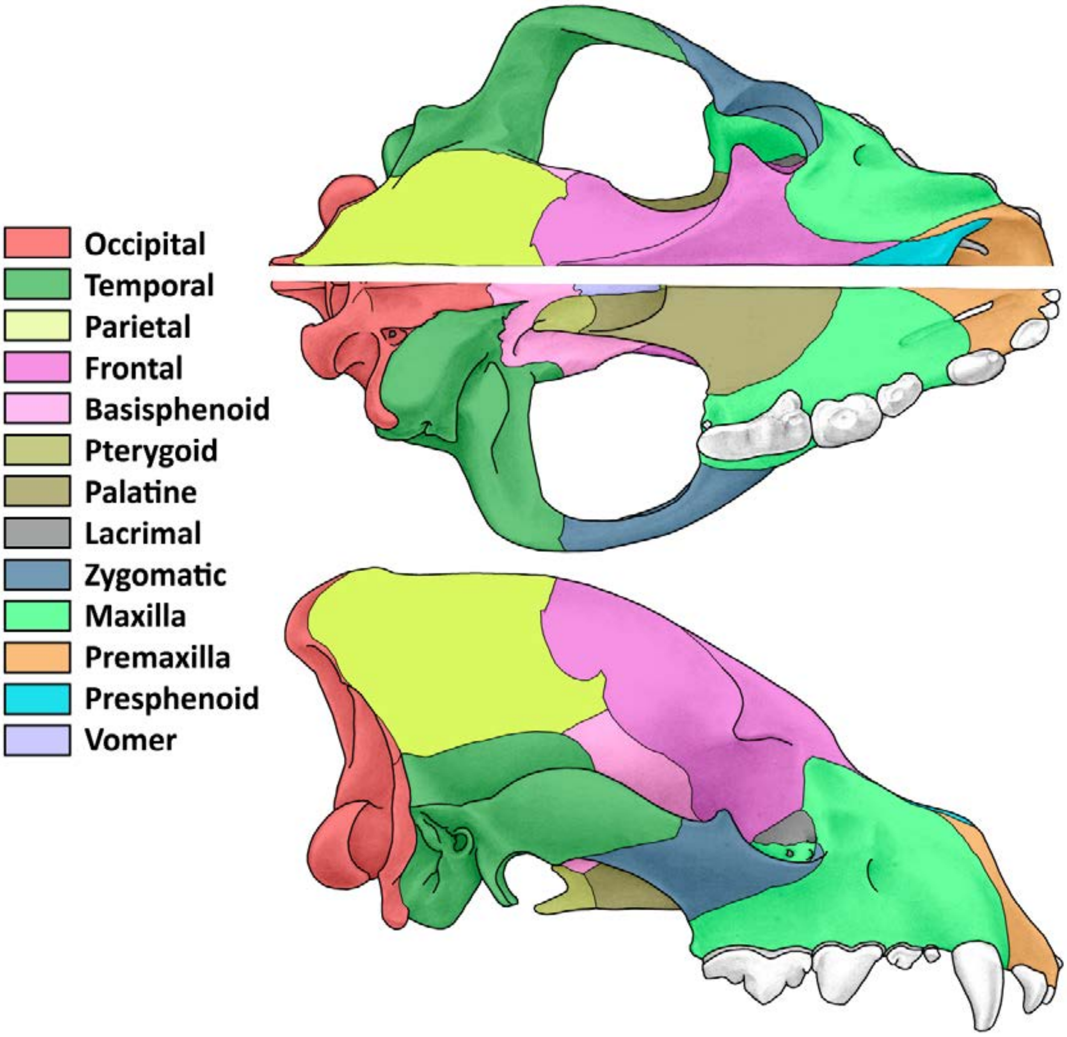

Figure 1.7: Hyaenid skull bones in dorsal, ventral and lateral views. Image modified from Werdelin and Solounias (1991).

missing or very reduced. The permanent dental formula for bone-cracking hyaenids is 3.1.4.1/3.1.3.1. The carnassials (P4 and m1) are very powerful and shifted far back to the point of exertion of peak pressure on the jaws, thanks to the absence of the second and third molars (both upper and lower). The remaining premolars are wide and robust, usually with a well-developed central cusp but low and blunt accessory cusps. Bone-cracking hyaenids rely on the premolars for breaking bones (thanks to the above-mentioned features) instead of the molars (like canids do). The canines are short, thick and robust, and the incisors characteristically possess two parallel cingula on their lingual face.

The myrmecophagous skull, present in *Proteles* (Fig. 1.8d), displays a dog-like morphology. On one hand, it displays the common hyaenid traits, such as the enlarged tympanic bulla (which is even proportionally larger than in the remaining hyenas). On the other hand, the skull of *Proteles* lacks the sagittal crest, the elongated frontal sinuses, and the wide and opened zygomatic arches that are characteristic of other hyenas, and unlike the latter, it further displays a longer muzzle. As a result of these features, the skull is less convex in lateral view. The mandible, in turn, is shallow and thin, with a low coronoid process, and a shallow masseteric fossa. The dentition is even more distinctive, being characterized by reduced and widely-spaced peg-like unicuspid cheek teeth that contrast with the still large canines. It generally displays the aforementioned general dental formula of hyaenids, although some specimens lack one or several of the anterior premolars.

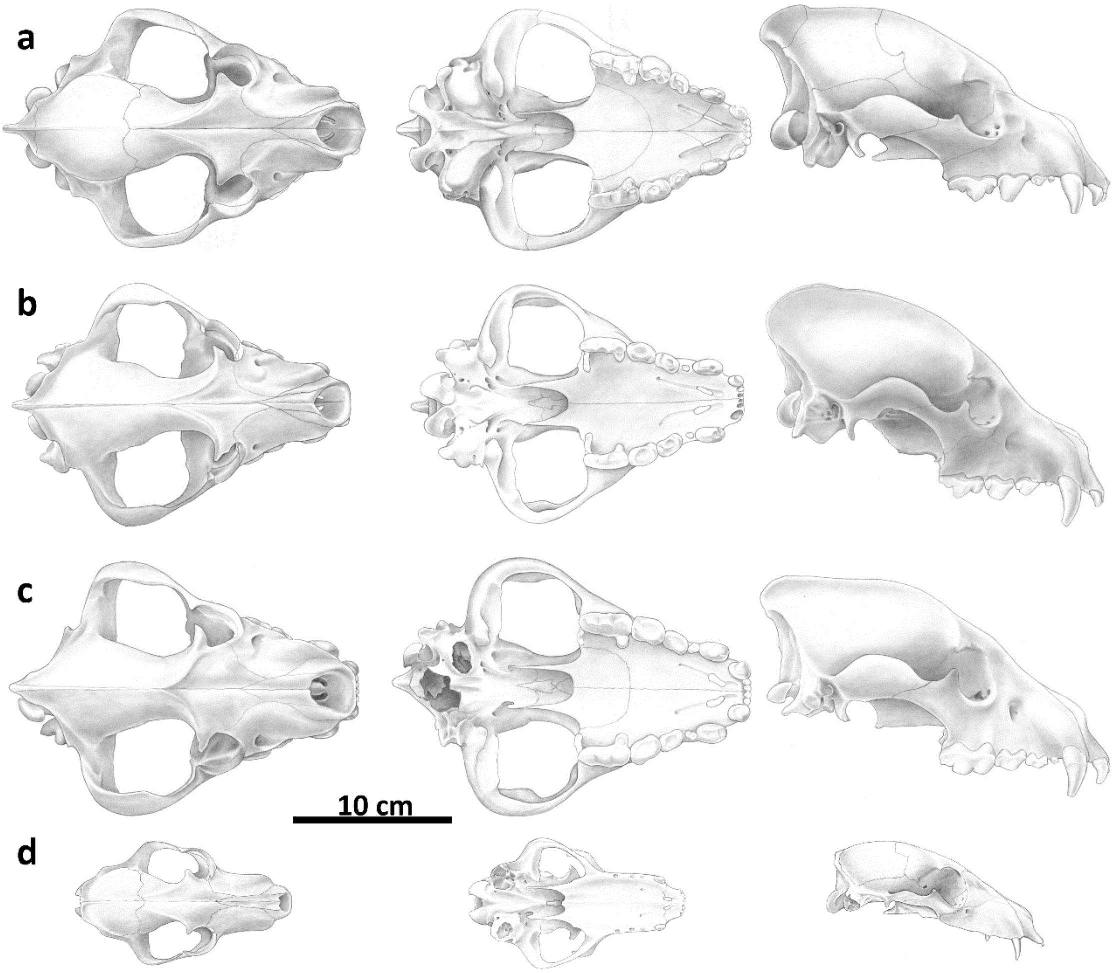

Figure 1.8: The skull of the extant hyenas in dorsal, ventral and lateral view. a, *Crocuta crocuta*; b, *Hyaena hyaena*; c, *Parahyaena brunnea*; d, *Proteles cristata* (reproduced from Werdelin and Solounias, 1991).

As mentioned above, the tympanic bulla is very distinctive of hyaenids, which is not surprising given that this anatomical structure has great relevance in the taxonomy and systematics of the Feliformia clade (e.g., Gregory and Hellman, 1939; de Beaumont, 1969a, Hunt, 1987). The bulla is part of the temporal bone, being located before the mastoid process and enclosing the middle ear. In carnivorans, it is formed by three or four different elements (Hunt, 1974): the ectotympanic, the rostral entotympanic, and the caudal entotympanic(s).

The ectotympanic and entotympanic have different evolutionary origins: the former is homologous to the angular bone of "reptiles", whereas the second corresponds to a cartilaginous ossification that is only present in mammals. In the Feliformia, the caudal entotympanic enlarges posteriorly during ontogeny, thereby forming the inflated bulla. The septum bullae is formed in the middle due to the union of the caudal entotympanic and the ectotympanic, dividing the bulla into two chambers. It was considered in the past that hyaenids had a single chamber (Flower, 1869), but in fact, they have two, being the ectotympanic hyperdeveloped, with the entotympanic pushed close to the mastoid process (Hunt, 1974). This character has allowed to secure the inclusion of several fossil taxa (such as *Plioviverrops* or *Thalassictis*) within Hyaenidae, as they present an intermediate stage (Winge, 1895; de Beaumont, 1964, 1969b; de Beaumont and Mein, 1972; Hunt, 1974; Solounias, 1981)

Postcranium. The postcranium (or postcranial skeleton, Fig. 1.9) includes all the bones placed behind the skull, thereby including the axial skeleton (vertebrae and ribs) and the appendicular skeleton (forelimbs and hindlimbs). The postcranial skeleton of different extant hyaenid genera is quite similar, except for differences in bone stockiness and interlimb proportions.

The forelimbs are connected to the axial skeleton through the thoracic girdle (scapulae) and are formed by the humerus, the radius, the ulna, the carpals, the metacarpals, and the manual phalanges. The hindlimbs are united to the axial skeleton through the pelvic girdle, formed by the coxal bones (ilium, ischium, and pubis), and include the femur, the tibia, the fibula, the tarsals, the metatarsals, and the pedal phalanges. All extant hyenas possess longer forelimbs than hindlimbs, unlike canids. Hyaenids, to some extent, are digitigrade, with the fore- and hindpaws possessing both four digits and supporting bulging paw pads. The distal phalanges of the fingers (the claws) are not protractile, unlike those of felids and viverrids. The long bones are generally more curved in hyenas than in other Feliformia, more closely resembling those of canids, although more robust. In the humerus, hyaenids lack both a supracondylar foramen (present in felids) and a supratrochlear foramen (present in canids). The stockiest and less cursorial extant hyaenid is the spotted hyena, which displays more robust limbs than the remaining genera. The curved and stocky girdles further resemble more closely those of canids, rather than the more slender, straight and elongated girdles of felids.

The axial skeleton has a total of 47–58 vertebrae (Ewer, 1973, Evans, 1993): 7 cervical, 15–16 thoracic, 4–5 lumbar, 2–4 sacral, and 19–26 caudal. They show limited mobility, even in the cervical area, which is enlarged and robust to maintain the powerful muscles involved in the bone-crushing system (except in *Proteles*). The atlas has wide wings, with large muscular insertions. The axis is thick and possesses a high spinal process as compared to felids and canids. The ribs articulate with the thoracic vertebrae. Hyenas have an additional couple of ribs compared to canids. Finally, hyenas lack a baculum (os penis), which is generally present in other carnivorans.

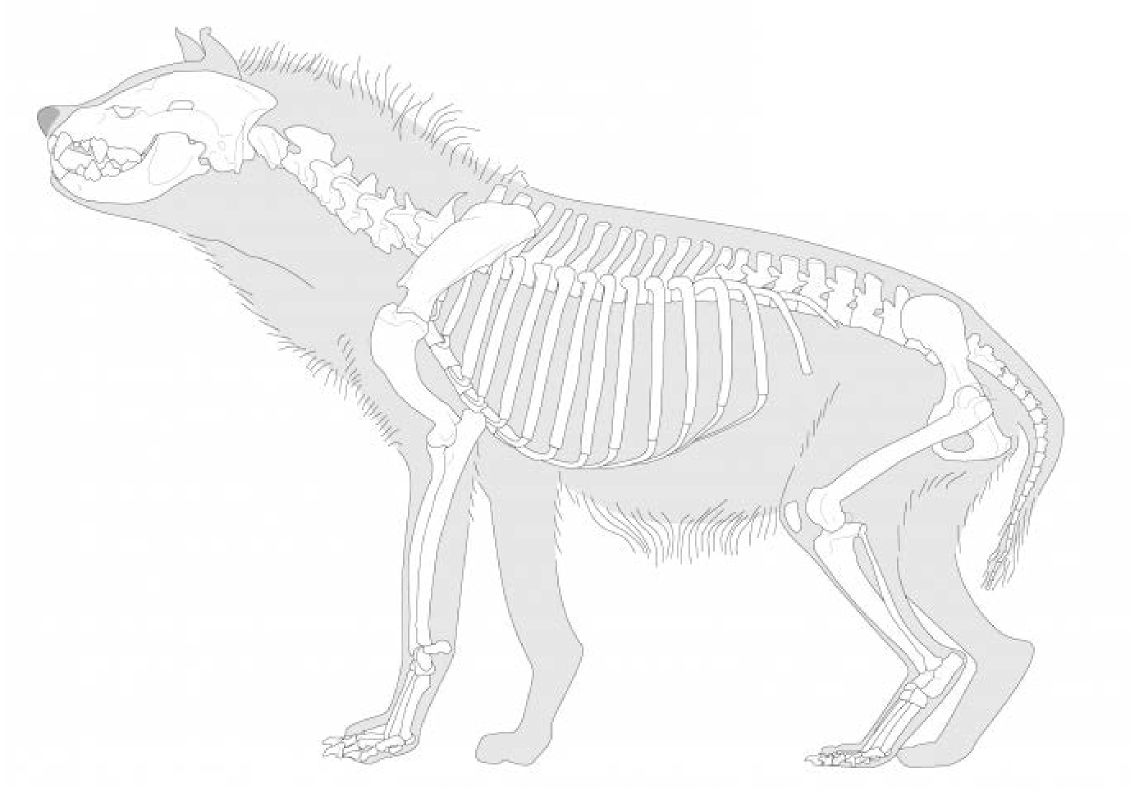

Figure 1.9: Complete skeleton of a spotted hyena (image made by Michel Coutureau and Cédric Beauval ©2004 ArchéoZoo.org).

Nervous system

Given the scope of this dissertation, the considerations provided below for the central neural system (brain and spinal cord) will be focused on the external morphology of the brain. Considering that the general brain anatomy is similar in all carnivorans, the general descriptions and images provided below are mostly based on Evans and Lahunta (2003), with only a few specific details for hyaenids (Holekamp et al., 2007; Arsznov et al., 2010; Sakai et al., 2011).

The brain (encephalon) itself is composed of billions of neurons and glial cells that form the gray and white matters. Neurons accumulate in nuclei and also in the cortex that covers the brain. White matter consists mainly of myelinated axons. On a macroscopic scale, the brain is divided into three large regions: the cerebrum, the cerebellum, and the brainstem.

Cerebum. The cerebrum (Fig. 1.10) is formed by the right and left cerebral hemispheres, separated by the longitudinal fissure except at the inner base, where they are united by the corpus callosum, the rostral commissure, the hippocampus and the fornix. Each hemisphere is composed of the cerebral cortex on the surface and white matter underneath; each one is composed of other minor structures, such as the rhinencephalon. There are three different kinds of cortex: the archicortex, which is associated with the hippocampus and the rhinencephalon; the paleocortex, with three layers, and also related to the rhinencephalon; and the neocortex, which is the most extensive. Morphologically, the surface or cortex features grooves (sulci) that separate elevated bands (gyri), making a visual pattern different in each species.

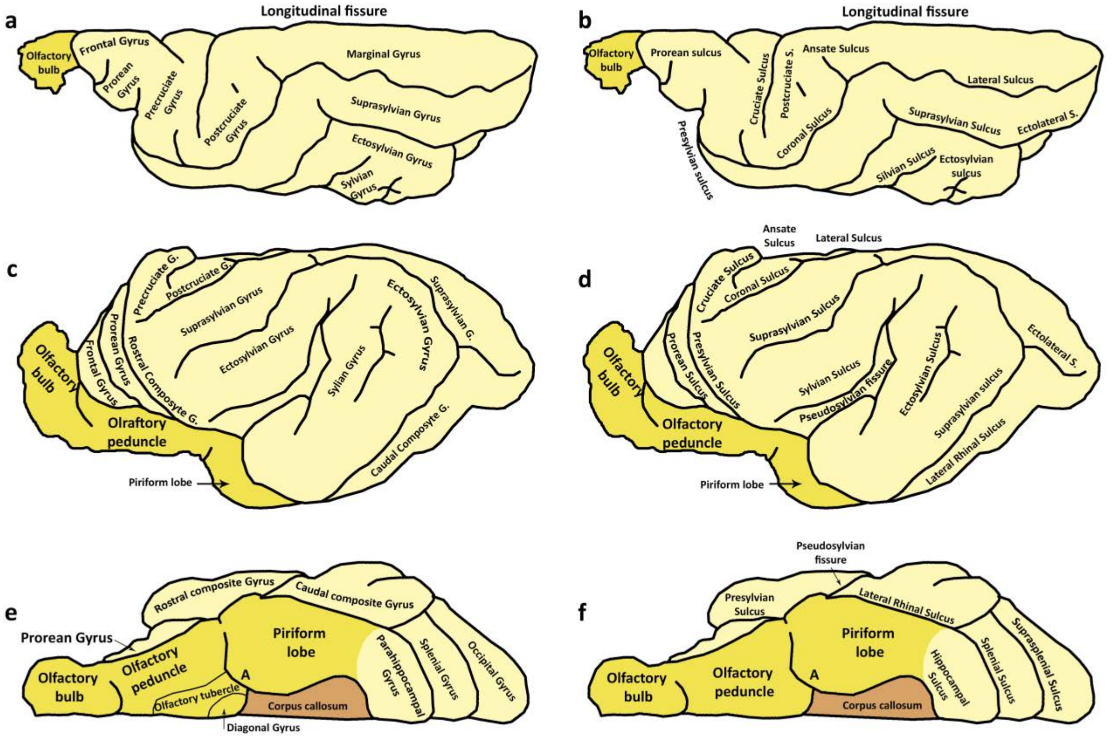

Figure 1.10: Schematic illustration of gyri, sulci and type of cortex of a hyaenid cerebral surface. a, Dorsal gyri; b, dorsal sulci; c, lateral gyri: d, lateral sulci; e, ventral gyri; f, ventral sulci. Neocortex is pale yellow, rhinencephalon (which has archicortex and paleocortex) is brighter yellow, and major white matter bundles are colored brown. In the piriform lobe of the ventral view, A marks the location of the amygdala.

The rhinencephalon is the ventral region of each hemisphere, separated from the neocortex by the lateral rhinal sulcus, and it is related with olfaction, memory and emotional behavior. In turn, the rhinencephalon is divided into three portions: the basal part, which includes the olfactory bulb; the limbic part, which is formed by the hippocampus, and the septal part. The olfactory bulb, located rostrally, is united to the cerebrum by the olfactory peduncle; both the olfactory bulb and the peduncle are hollow and filled with cerebrospinal fluid. The bulb is formed by seven histologic layers, and it is a region where all the olfactory nerves end. There are two other minor regions of the rhinencephalon: the olfactory tubercle, related to the hypothalamus (in the brain stem); and the pyriform lobe, which concerns conscious olfaction. The amygdala is placed in the piriform lobe. The hippocampus is located under the corpus callosum between both hemispheres, being functionally related to long-term memory formation as well as spatial memory. The cerebral neocortex is composed of six layers and organized into vertical columns, being all the neurons within the column responsive to the same specific feature of a particular stimulus. The white matter that lies under the neocortex is generally made of the neocortex axons, which can be either corticopedal (comes in from the spine) or corticofugal (leaves from the cortex). The corpus callosum links corresponding neocortical regions of the two hemispheres, making of the cerebrum a single cognitive center.

The neocortex is also divided into functional regions (Fig. 1.11), which can vary in thickness and axonal connections, depending on the role of each area. The primary somatosensory area receives tactile, kinesthetic (muscle movements sense), and nociceptive axonal projections (potentially harmful stimuli, like pain) from ventral caudal thalamic nuclei via the internal capsule, and it is somatotopically organized with head representation facing rostrally. Close to the tongue and pharynx somatosensory area of the previous region, there is a gustatory area, which is also connected to the rhinencephalon. The visual area is placed in the occipital lobe, and it receives input from the lateral geniculate nucleus; the area centralis of the retina occupies an expanded zone in this area. The primary auditory area is located in the temporal lobe, around the middle ectosylvian sulcus (receives tonotipic input, organized by frequency), the caudal ectosylvian sulcus (receives nontonotopic input) and the sylvian gyrus (auditory association). The frontal association cortex, which is particularly developed in the spotted hyena, occupies the frontal pole. It processes emotional status as well as the cognitive perception in order to decide, plan and organize the behavior to achieve goals. This goal-achievement behavior also involves short-term memory and behavioral suppression (e.g., of inappropriate emotional behavior). It also has broad connections to the association and premotor cortex, the cerebellum, the hypothalamus, and the limbic system. The premotor cortex is placed between the prefrontal cortex and the motor cortex and acts as a nexus between them, passing projections from the former to the latter. It is also related to movement learning and rapid sequential movement. The supplementary motor area is adjacent to the premotor cortex and is particularly active when observing movements before them. The motor cortex is placed caudally from the previous two and is related to basic movement, being somatotopically organized with respect to joint movement. It executes simple, automatic or habitual movements in response to triggering stimuli (an input), but it can also execute complex or previously learned movements with the aid of the premotor cortex.

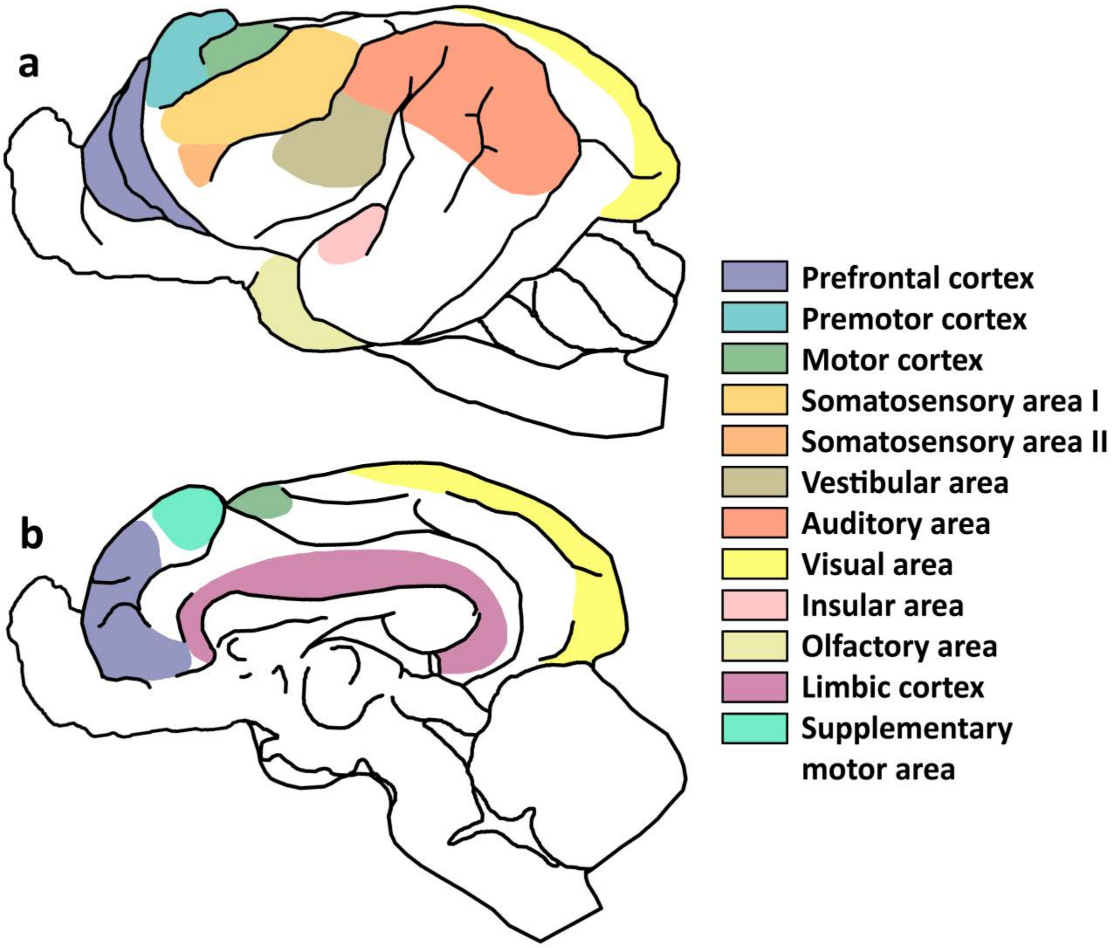

Figure 1.11: Functional regions in the neocortex of the brain. a, lateral view; b, medial view.

Finally, the telencephalic basal nuclei consist of accumulations of gray matter outside of the cortex (inside the white matter and close to the piriform lobe) that are linked or connected to one or more areas of the neocortex or the rhinencephalon. They include the nucleus accumbens, the caudate nucleus, the putamen, the pallidum, the endopeduncular, the claustrum, and the amygdala.

Brainstem. The brainstem (Fig. 1.12) occupies the most basal and caudal part of the brain. It is the arising area of all the cranial nerves except for the olfactory one. The brainstem is connected to the cerebrum through the internal capsule and to the cerebellum by the cerebellar peduncles. The brainstem is also subdivided into regions, being these (from caudal to frontal) the medulla oblongata, the pons, the midbrain and the diencephalon.

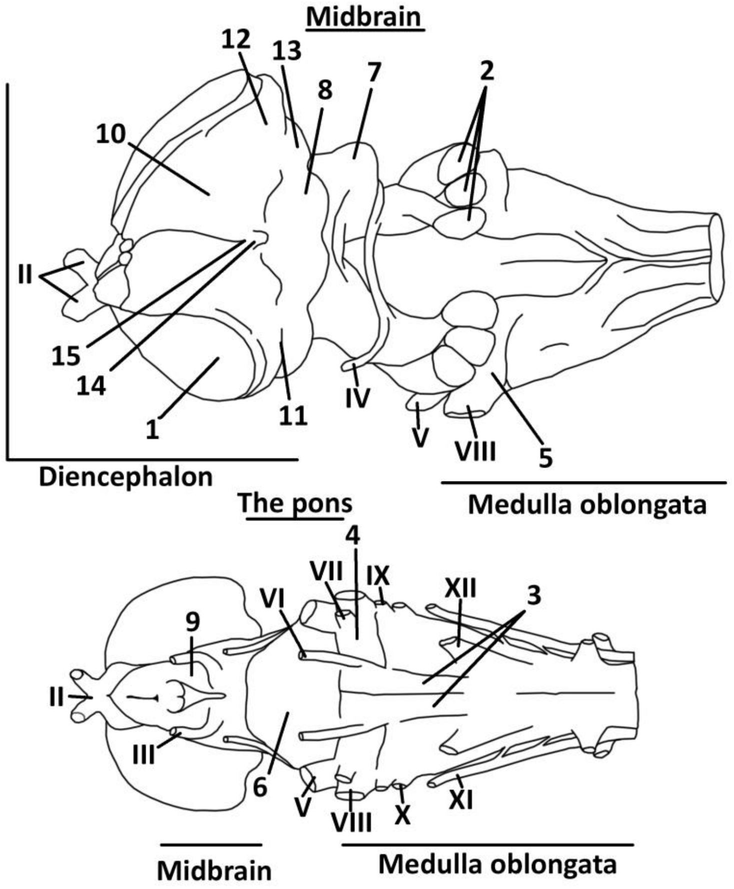

Figure 1.12: Dorsal and ventral views of the brainstem. 1, internal capsule; 2, cerebellar peduncles; 3, piramids; 4, trapezoid body; 5, cochlear duct; 6, transverse pontine fibers; 7, caudal colliculi; 8, rostral colliculi; 9, crus cerebri; 10, thalamus; 11, metathalamus; 12, lateral geniculate body; 13, medial geniculate body, 14, pinneal gland; 15, habenula; II, optic nerve; III, oculomotor nerve; IV, trochlear nerve; V, trigeminal nerve; VI, abducent nerve; VII, facial nerve; VIII, vestibulocochlear nerve; IX, glossopharyngeal nerve; X, vagus nerve; XI, accessory nerve; XII, hypoglossal nerve. (Image redrawn from Evans and Lahunta, 2013).

The medulla oblongata is placed caudally (Fig. 1.12), connected to the spinal cord, and is characterized by bilateral and longitudinal bands of white matter, the pyramids, which are parallel to the ventral midline. The rostral end of it is made by the trapezoid body. Seven of the cranial nerves (VI-XII; Fig. 1.12) arise from different parts of it. Histologically it is made of gray matter nuclei (mainly of the cranial nerves), white matter tracts (formed mainly by axons of the cranial nerves and the cerebellum) and the mixed reticular formation. The caudal end of the medulla oblongata serves as the junction with the spinal cord, sharing features with it, but it also has minor structures (such as the pyramids and several nuclei) and connections (such as the caudal cerebellar peduncle). The rostral end of the medulla oblongata includes the majority of the cranial nerve connections as well as the cochlear duct (which is the sense organ for hearing). The latter has several nuclei and elements that from also the trapezoid body.

Besides this, the medulla oblongata functions are also related to a wide variety of sensory and involuntary motor functions, such as heart rate.

The pons is placed rostral to the medulla oblongata (Fig. 1.12) and is divided between the tegmentum (dorsally) and the transverse pontine fibers (ventrally). The fibers of this area merge from the pontine nucleus (which is inside this ventral region) and form the middle cerebellar peduncle. The tegmentum is similar to the medulla oblongata, and also has a few nuclei inside it. One major cranial nerve arises from the pons (CN V; Fig. 1.12), and all the nuclei associated with it are located in this area. The major functions of the pons are related to voluntary but simple acts (sleep, respiration, swallowing, etc.).

The midbrain which is placed above the pons (Fig. 1.12) is essentially divided into two regions, which surround the mesencephalic aqueduct (a connection channel between the diencephalon and the pons). The area dorsal to the aqueduct is covered by the tectum, which is formed by paired rostral and caudal colliculi (gray matter nuclei) and their respective commissures; the colliculi main functions are related to sound and vision respectively. The other main region of the midbrain is formed by the cerebral peduncles, which are paired and ventral to the aqueduct, and are subdivided into three regions; from dorsal to ventral: the tegmentum, the substantia nigra, and the crus cerebri. They are formed essentially by gray matter nuclei and white matter, and connect the midbrain with the thalamic nuclei (cerebrum); their function is related to motor movements and skills, as well as balance and posture maintenance. Also, two of the cranial nerves (III, IV) are placed in this area (Fig. 1.12).

The diencephalon is the most frontal region of the brainstem (Fig. 1.12), which is connected to both cerebral hemispheres by the internal capsule. The diencephalon is formed by five regions: thalamus, metathalamus, hypothalamus, epithalamus and subthalamus. The thalamus is a structure closely linked to the cerebral cortex, with continuous information exchange between them. It is constituted by several nuclei, and it is considered to act as a relay between different subcortical areas and the cerebral cortex. All senses have their thalamic nuclei in here (except for the olfactory system), which receive sensorial information that is sent later to the cortex. The thalamus also has several other functions, such as regulating sleep and wakefulness. The metathalamus is formed by two geniculate bodies or nuclei (medial and lateral), similar to the thalamus, but specialized in hearing and vision. The hypothalamus is formed by several small nuclei and makes the ventral part of the diencephalon. It is also part of the limbic system, and one of its most important functions is to link the nervous system to the endocrine system through the pituitary gland. Other major functions are related to metabolic processes (body temperature, hunger…) as well as synthesizing neurohormones. The epithalamus is formed by the pineal gland, as well as the habenula and all its associated tracts. It basically connects the limbic system with other parts of the brain and secretes hormones. Finally, the subthalamus is formed by the zona incerta, the subthalamic nucleus, and white matter, and its primary functions are related to movement inhibition.

Cerebellum. The cerebellum (Fig. 1.13) can be divided regionally into a median vermis and two bilateral hemispheres. As a whole, it coordinates posture and movement by regulating muscle tone and joint action. As in the cerebrum, the cerebellum can also be divided morphologically in several hierarchies into lobes and lobules separated by fissures. The surface can also be divided into folia (ridges) and sulci (grooves). The primary division is made by the uvulonodular fissure into the flocculonodular lobe and the cerebral body (placed in the ventral part of the cerebellum). The function of the former is to correct vestibular reflex errors, whereas the latter is more complex, being also subdivided into the rostral and the caudal lobes, with different functions. The rostral lobe is connected to the spinal cord and regulates posture and gait, whereas the caudal lobe is connected to the forebrain and affects voluntary movement.

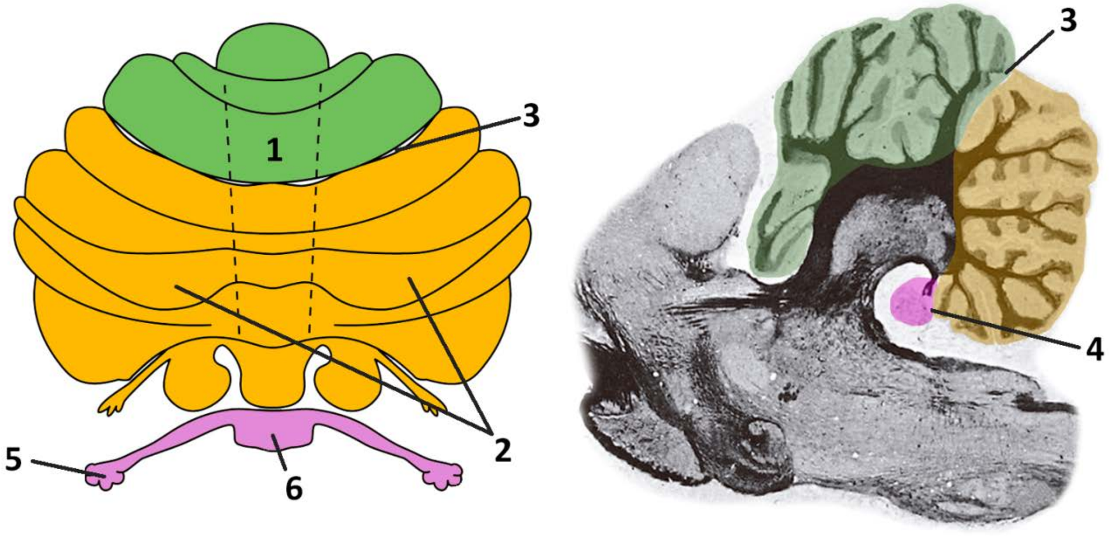

Figure 1.13: Caudal and medial view of the cerebellum. The different lobes are colored in both views: flocculonodular lobe (pink), rostral lobe (green), caudal lobe (yellow). 1, median vermis; 2, bilateral hemispheres; 3, primary fissure; 4, uvulonodular fissure; 5 Flocculus; 6, Nodullus. (Left image modified from OpenStax College, CC BY 3.0, Wikimedia Commons; right Image modified from Jardim-Messeder et al., 2017).

Histologically, the cerebellum is formed by cortex, white matter, and nuclei, in a similar way to the cerebrum. The cerebral cortex is composed of three layers of gray matter on the surface, with Purkinje cells, and their axons are the only output of the cortex itself, which terminate in the cerebellar or vestibular nuclei. The white matter inside the cerebellum is called the arborvitae; it has the shape of three branches and is composed of a lamina in each folium and a center called the cerebellar medulla. Finally, three cerebellar nuclei are inside the white matter; their axons are the only ones that leave the cerebellum, sending the input received from the cerebellar cortex.

The cerebellum is connected to the brainstem bilaterally by three cerebellar peduncles that are composed entirely of cerebellar axons, which can be either afferent (input) or efferent (output).

1.1.4. Biology and behavior

Among living hyenas, the spotted hyena is the most extensively studied one from the viewpoint of ecology (e.g., Kruuk 1970, 1972a; Frank, 1986a, b; Mills, 1990; Holekamp and Smale, 1993; Holekamp et al., 1997, 1999), followed by brown hyenas and aardwolves. Striped hyenas are not well known, in spite of the fact that they have the widest geographical range, and the limited data available result mostly from in-depth studies of hyaenids as a whole in the Southern Kalahari Desert and the Serengeti, with some minor studies in Asia (Kruuk, 1976; Skinner and Ilani, 1979; Skinner et al., 1986; Mills, 1990). This contrasts with the situation of the brown hyena, which is restricted to south of Africa, but whose behavior has been investigated throughout its whole range (Eaton, 1976; Mills, 1977, 1978, 1982a, 1990). The rareness of the aardwolf's diet is reflected on its absence in many studies, but it has further led to a special focus on it, resulting in some specific studies (Bothma, 1971; Richardson, 1987a, b; Anderson et al., 1992; Richardson and Levitan, 1994).

Distribution, habitat and conservation status

Hyenas currently inhabit Africa, parts of the middle East and southwestern Asia (Fig. 1.14), occupying a large variety of habitats (deserts, thick bush, swamps, montane forests, and open savannas). The striped hyena has the widest distribution (Rieger, 1979; Mills and Hofer, 1998): Africa from the Equator to the Mediterranean Sea, reaching both eastern and western limits of the continent, but avoiding the central Sahara and Arabic Deserts; and Asia from Nepal and India in the east, the Caucasus in the north, and Turkey to the west. However, the distribution of striped hyenas in these areas is patchier instead of continuous (Mills and Hofer, 1998). They rely to a great extent on water sources (Rieger, 1979), and tend to inhabit rugged and arid habitats or light thorn bush countries in Asia, avoiding areas with long periods of frost or snow, reaching maximum altitudes of 3300 m in Pakistan (Roberts, 1977), given that they can stand low temperatures (-20 ºC; Heptner and Slodskij 1980). In Africa, they habit more diverse areas, including open savannas and woodlands, as well as arid regions and ruggy-bushed mountain areas (Rosevear, 1974; Kruuk, 1976; Leakey et al., 1999; Wagner, 2006).

The second most widely distributed species is the spotted hyena, which inhabits throughout Africa south of the Sahara Desert (i.e., sub-Saharan Africa), except for the dense rainforest areas in the Central Africa and a large part of South Africa, where it was exterminated (Mills and Hofer, 1998; Holekamp and Kolowski, 2009). The area with the highest density of spotted hyenas is located in East Africa, in the plains of Kenya and Tanzania (Kingdon and Hoffmann, 2013). They live in many different habitats, including savannas, swamps, woodlands, and montane forest, reaching even 4000 m of altitude (Kruuk, 1972a; Young and Evans, 1993).

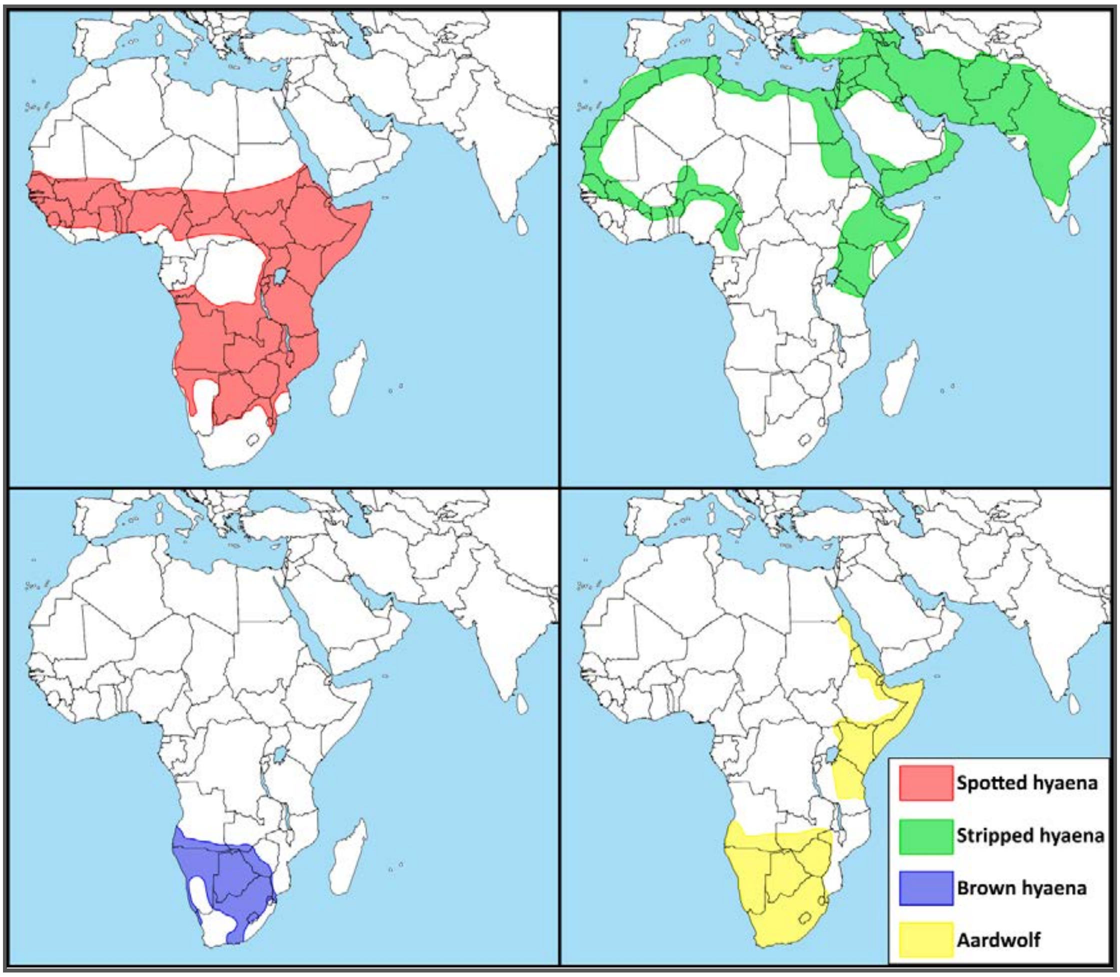

Figure 1.14: Current distribution of all four extant hyena species (Data taken from Holekamp and Kolowski, 2009).

The next most extended hyena is the aardwolf, with two separated distribution areas (Koehler and Richardson, 1990; Mills and Hofer, 1998; Holekamp and Kolowski, 2009; Kingdon and Hoffmann, 2013): one located in East Africa, being the north of Tanzania the southern limit, Eritrea to the north (they even reach the southern part of Egypt), lake Victoria to the west, and the Indic Ocean to the east; and a second distribution area, located in southern Africa, and limited to the north by Zimbabwe and the South of Angola. Aardwolves, in both areas of distribution, inhabit open grassy plains or bushy countries, avoiding desert areas (as they highly rely on water sources), as well as forests (Smithers, 1983; Koehler and Richardson, 1990; Skinner and Chimimba, 2005; Holekamp and Kolowski, 2009).

Finally, brown hyenas are the rarest ones. They live only in the south of Africa, their range extending northward up to Namibia, Botswana and Zimbabwe (Smithers, 1971, 1983; Skinner, 1976; Smithers and Wilson, 1979; Mills and Hofer, 1998). They can be found in a large variety of habitats, from savannah and bushveld in the Transvaal (Skinner, 1976) to arid and semi-arid areas in the Kalahari and Namibia (Smithers, 1983), as they can habit areas with very low annual rainfalls (Mills and Hofer, 1998).

Diet and feeding behavior

Despite their low extant diversity, hyenas display a variety of feeding behaviors, from active pack hunter to solitary foragers (Houston, 1979). Also, their dentition is adapted to both meat-eating and bone-crushing (in the three larger species, but especially in *Crocuta*), with the exception of *Proteles*, which displays a very reduced dentition (Mills, 1990). The four species of living hyenas forage (e.g., travel long distances looking for food) in a wide variety of forms, and all the large species scavenge as much as they can (doing so more often than any other extant carnivoran).

***Diet*.** Spotted hyenas eat almost everything they can, and scavenge to a large extent, although they also actively hunt (more than it was believed in the past; Johnston, 1884; Eloff, 1964; Kruuk 1966, 1972a; Mills, 1990; Bothma, 1998; Holekamp and Kolowski, 2009; Kingdon and Hoffmann, 2013). The information currently available is rather varied, such that not many generalities can be made about the routines of this species, with the various studies being based on different areas. Their diet varies considerably from region to region, depending on the availability of prey, resulting in marked differences in the proportion of killing vs. scavenging, prey species, or non-common dietary elements. Spotted hyenas hunt at least the half of the carcasses they eat (reaching the 96% in the Ngorongoro crater; Kruuk, 1966; 1972a; Mills, 1978), being the main producers of carcasses in areas such as the Serengeti, the

Ngorongoro crater, or the Central Namib desert (the latter case is due to the lack of other large predators (Kruuk, 1966; Tilson and Henschel, 1986; Bothma, 1998). They mainly feed on large ungulates within a body mass range of 56-182 Kg (Höner et al., 2005; Hayward, 2006), but the most frequent prey species vary among regions (see table 1.1). However, they can feed on smaller mammals, reptiles, and even termites or fruits (and even practice cannibalism; Pienaar, 1969) if main preys are lacking (Mills, 1978, 1990; Bothma, 1998). Spotted hyenas can also take advantage of calving seasons, leading to an increase in the proportion of calves eaten (especially for the main prey of the region; Mills, 1990; Bothma, 1998). Finally, spotted hyenas regionally differ in the number of bones carried to their dens (they are carried more often in East Africa than in South Africa; Sutcliffe, 1970).

Table 1.1: List of the most common species that spotted hyena prey on in each studied region, with percentages when provided (Kruuk,1972a; Smuts, 1979; Tilson et al., 1980; Mills, 1984, 1990; Cooper, 1990a; Henschel and skinner, 1990; Gasaway et al., 1991; Sillero-Zubiri and Gottelli, 1992; Hofer and East, 1993a; Mills and Biggs, 1993; Bothma, 1998; Cooper et al., 1999; Höner et al., 2002, 2005)

Location	Prey species	Location	Prey species	Location	Prey species
Serengeti N.P. (Tanzania)	Wildebeest, Thomson's Gazelle and Plains Zebra	**Ethosa N.P. (Namibia)**	Springbok	**Aberdare Mountains (Kenia)**	Bushbucks, Sunis and African buffalo
Ngorongoro crater (Tanzania)	Common Wildebeest, Thomson's Gazelle and Plains Zebra	**Namib Desert (Namibia)**	Gemsbok (>80%), followed by Zebras.	**Niokolo Koba N.P. (Senegal)**	African Buffalo
Kruger N.P. (South Africa)	Impala (67,5%), Burchell's Zebra and Blue Wildebeest.	**Chobe N.P. (Botswana)**	Impalas and Plain zebras.	**Faro N.P. (Cameroon)**	Buffon's kob
Southern Kalahari Desert (South Africa)	Gemsbok, Common Wildebeest, Springbok.	**Masai Mara (Kenia)**	Topis and Thomson's Gazelle		

Contrary to spotted hyenas, striped hyenas are not efficient hunters and rely basically on foraging (Mills, 1990). They feed mainly on carrion, especially the bony remains of carcasses (Riger, 1979). They are also much more omnivorous and eat small vertebrates, insects, fruits or even human wastes (Flower, 1932; Harrison, 1968; Ilani, 1975; Kruuk, 1976; Macdonald, 1978; Leakey et al., 1999; Wagner, 2006). As in spotted hyena, striped hyenas also display regional dietary differences that in part depend on resource availability, (Kruuk, 1976). As an example, the diet of striped hyenas in the Negev desert is supported by desert dates (Bouskila, 1984), whereas in the Serengeti it is mainly supported by one variety of wild plum (Kruuk, 1976; Palgrave, 2002).

Brown hyenas, are also generalist, opportunistic and scavenging carnivores that eat almost everything they can, and this include fruits, insects, birds' eggs (Eaton, 1976; Skinner, 1976; Mills, 1978, 1982, 1990; Mills and Mills, 1977; Owens and Owens, 1978; Skinner and Van Aarde, 1981; Siegfried, 1984; Stuart and Shaugnessy, 1984; Maddock, 1993; Burgener and Gusset, 2003; Mills and Maude, 2005; Kuhn et al., 2008). Their feeding behaviors are well documented in their two distribution areas, the Kalahari and the Namib Desert (Eaton, 1976; Mills, 1977, 1978, 1990). In the Kalahari Desert, they scavenge almost (96%) all the meat they eat (Mills, 1990), the carcasses mainly belonging to blue wildebeest and gemsbok (Fig. 1.15; Mills, 1982a). They strongly complement this primary resource with insects, plants, and fruits, like the tsamas, the gemsbok cucumbers or the wild cucumber, which are low on nutritional volume but high in vitamins (Mills, 1978). In contrast, in the Namib desert, resident brown hyenas mostly feed on seal remains (up to 76%, mainly seal pups), followed by seabirds (Siegfried, 1984; Bothma, 1998). This is due to the presence of many seal rockeries along the shore area, where almost all of the brown hyenas in the Namib Desert concentrate. One of their favorite supplementary items are ostrich eggs, which are eaten when available (Skinner, 1976; Mills, 1990). Brown hyenas are the only large carnivorans able to open them easily with their bite, whereas spotted hyenas and lions must rely on other methods to do so (Mills, 1990).

Figure 1.15: Brown hyena carrying a cascass in the Kalahari desert (Photo by Derek Keats, CC-BY 2.0, Flickr.com).

Finally, the aardwolf’s diet is based almost solely on termites from a single genus, *Trinervitermes*, with the occasional small addition of termite species from other genera, dung beetles, flying ants and even, in rare cases, leopard tortoises (Bothma, 1971). Aardwolves can lick up to 300,000 termites per night (Richardson and Levitan, 1994), including the two types of termites that are in the open during night-time (workers and soldiers). *Trinervitermes* spp. typically forage nocturnally the surface of the ground, as they are not usually attacked due to their highly effective chemical defenses. Since these termites must not be dug out, the only myrmecophagous adaptation that aardwolves display to ingest them consists in stomach resistance to their toxicity (Anderson et al., 1992; Richardson and Levitan, 1994). It is considered that the distribution of aardwolves is limited by the distribution of these termites (Kruuk, 1972a; Richardson, 1987a, b). The most commonly eaten species are *Trinervitermes bettonianus* (in Eastern Africa) and *Trinervitermes trinervoides* (in South Africa), although this pattern may vary due to climatic conditions. Thus, in the Northern Cape province and the Namib Desert, aardwolves consume instead *Hodotermes mossambicus* during the winter since the latter are more active (and hence forage outside) when temperatures are colder (Richardson, 1987a, b).

***Foraging and hunting*.** Due to the disparity of food resources consumed by each species, their foraging and hunting abilities are also different and further may vary depending on the region (Mills, 1990).

The foraging habits of spotted hyenas are well studied in many different locations, but in general, their foraging behavior is focused on the look for preys to hunt or of carcasses to eat. They forage in small groups (variable in number from region to region; Mills, 1978, 1990; Cooper, 1991; Bothma, 1998; Holekamp and Kolowski, 2009; Kingdon and Hoffman, 2013). Social status is important to determine these foraging groups and their moving range; for example, males have to move greater distances when foraging or eat more low-quality food (Bertram, 1979). In spotted hyenas, hunting and foraging patterns are not driven by stealth, agility or speed, as in many other large predators such as big cats, but rather by a remarkable tenacity, aided by their fine smelling and hearing senses (Mills, 1990; Bothma, 1998). They can hear living prey from up to 2.4 km away and smell them (or carcasses) from up to 3 km downwind (as recorded in the Kalahari Desert; Mills, 1990), being able to follow scent trails, especially on damp ground (Mills, 1990). Sight is also commonly used when locating prey, especially in open, flat and rivered habitats, even at night, since they have an excellent nocturnal vision (Bertram, 1979). In fact, spotted hyenas tend to hunt at night, when these abilities are more reliable (Deane, 1962; Bertram, 1979; Mills, 1990) and represent a clear advantage over the prey. When hunting in group (which they normally do, because it increases the success rate; Kruuk, 1972b), the hunting party charges into a herd of herbivores, biting in groups or individually the legs or any other body part in reach of one of the fleeing animals until it is killed (Kruuk, 1966, 1972b). Social behavior is intrinsically related to group foraging and hunting parties, although solitary hunting may also occur, as reported from the Kruger National Park and the Southern Kalahari Desert (Kruuk 1966, 1972b; Bearder, 1977; Mills, 1990). Like African wild dogs, spotted hyenas hunt in long distance runs, until the prey gets exhausted. Prey selection among their flock is determined by species, age, numerical abundance, prey's antipredator behavior, and the hyena's ability (Mills, 1990). For example, when hunting gemsbok, spotted hyenas avoid subadult specimens because they run longer than either adults or offspring. The hunting flexibility of spotted hyenas, depending on each region and available resources, is most remarkable. This is best exemplified by large water areas, into which preys are driven, drown after a long chase, and subsequently carried to the shore to be eaten, thanks to their good swimming abilities (Child and Robbel, 1975).

Figure 1.16: A spotted hyena steals the prey from a cheetah in the Masai Mara (Photo by Adam, 2005, CC BY-NC 2.0, Flickr.com).

Kleptoparasitism also plays a big role in the foraging of spotted hyenas (Fig. 1,16; Kruuk, 1972a, Henschel and Skinner, 1990, Mills, 1990), as they easily discover the kills of other large predators such as lions, and readily steal their prey. Although there are several factors that play a role in kleptoparasitism, such as the presence of a male lion, in general hyenas have to double lions in number to mob them and be able to join the food, and can even steal completely the prey if they reach a 4:1 ratio (Bothma, 1998; Cooper, 1991).

In Africa, striped hyenas forage almost exclusively alone (Kruuk, 1976; Wagner et al., 2008), although sometimes they group in pairs or small groups while foraging (Rieger 1979; Bouskila, 1984). When foraging groups are formed, at least in the Negev desert, each individual immediately reports any kind of food found in their path to the other members (Kruuk, 1976; Skinner and Ilani, 1979; Bouskila, 1984). It is also known that they prefer foraging at night, with an erratic zig-zagging around the landscape that does not follow routines (Kruuk, 1976). In these night trips, they walk a mean distance of 19 km and eat 7–8 kg of food (Skinner and Ilani, 1979). Besides this, there is not much knowledge about the foraging habits of these hyenas, although they are supposed to be closest to those of brown hyenas (except for the more frequent killing behavior of the latter).

Brown hyenas do not spend as many resources or time hunting as spotted hyena (Bothma, 1998). They do hunt sometimes, but always small animals and in a much less elaborated way (they just chase and grab them; Mills, 1990). Brown hyenas forage and look for any kind of potential food source for long distances, but they do so in solitary, even despite the fact that they often socialize around carcasses (Mills, 1990; Bothma, 1998). Like spotted hyenas, brown hyenas have excellent hearing, smelling and night vision capabilities, which combined allow them to successfully find the needed resources (Mills, 1990). Smell is the major sense used to detect other predator's prey, scents or carrion, but the former can also be achieved thanks to acute hearing. The Kalahari Desert is the area where their foraging behavior is best known, and even within its boundaries, there are local differences in the number of resources spent in hunting (as brown hyenas hunt more in the center region than in the southern one). Brown hyenas typically make foraging paths that connect water and food resources, such as carcasses. The mean distance traveled when foraging during the night by brown hyenas oscillates between 20 and 30 km, but can change seasonally or due to weather conditions (Mills, 1990); for example, brown hyenas forage when other predators gather during the heavy rains (Owens and Owens, 1978). These patterns are somewhat different in the Namib Desert, due to the unique food resources (dead seal pups) of that area (Stuart and Shaughnessy, 1984).

The foraging behaviors of aardwolves are heavily driven by their myrmecophagous adaptations and focused on *Trinervitermes* termites. These hyaenids forage only at night, and they stop foraging if it begins to rain, as their food hide underground in that situation (Kruuk, 1972c; Bothma, 1998). They primarily locate termite patches following the scent upwind or by hearing at a distance of 1–2 m. Aardwolves forage alone in irregular paths with an average slow speed of 2–3 km/h when looking for patches, and an even slower speed of 1 km/h when they are feeding of the patches (Kruuk, 1972c; Richardson, 1987b). The amount of time spent in each termite patch, which are separated from each other by about 100 m, depends on its density; when they feed, they follow irregular routes through the patch while licking up termites (Bothma and Nel, 1980). The range of foraging is determined by the nutritional requirements and the termite density of the area, but aardwolves require up to 3,000 termite mounds per territory to survive (Richardson, 1987c).

Feeding**.** When eating, spotted hyenas are able to manipulate food with the forepaws, although they do not chew the food as other carnivores do (Van Valkenburgh, 1996), given that their stomachs digest the carcasses more efficiently. Although there is no fighting for the carcasses among members of the same clan, competition has made spotted hyenas eat very fast, being able to consume up to 30% of their body mass in a single meal (Kruuk, 1972a; Bearder, 1977). There are records of 30 members eating from the same carcass (Mills, 1990), and they can fully consume a carcass of a medium size prey in less than 30 minutes (Frank, 1986a). All these generalities are to some extent variable, depending on each region and their food resources.

Spotted hyenas do not normally store food in their dens (Bothma, 1998), although they do accumulate bones in there (Bearder, 1977; Mills and Mills, 1977; Henschel et al., 1979, Skinner et al. 1986; Lam,1992; Skinner, 2006). The amount of bones accumulated varies depending on the temporality of the den itself, such that permanent dens accumulate many more bones than temporal ones. There are exceptions regarding food storage, such as in the Kalahari Desert, where due to a lesser food availability hyenas cache food in waterholes, under bushes o in tall grass areas, whereas east Africa hyenas only do so in waterholes (Mills, 1990).

Striped hyenas store food more often than spotted hyenas, as a backup for times of food scarcity (Mills, 1990; Bothma, 1998). Their feeding and storing habits are based on the disposition of water, on which they depend. When feeding on a carcass, striped hyenas start at the end of the spinal cord, at the anus, as the buttocks are their preferred part of the body (Skinner and Ilani, 1979).

Brown hyenas also store food, including not only carcasses and bones, but also ostrich eggs, which they can easily carry for long distances (Mills, 1990). Brown hyenas may stock bones and ostrich eggs for a long term, whereas meat and carrion are normally eaten or recovered within 24 hours after storage (Skinner and Van Aarde, 1981; Skinner et al., 1992; Skinner, 2006; Kuhn et al., 2006). Brown hyenas usually eat alone, particularly when feeding on small preys, bones or old pieces of carcasses; however, sometimes several individuals gather to feed and socialize around a bigger carcass (Mills, 1990). Depending on the region, brown hyenas may show a strict hierarchy dominance (Owens and Owens, 1978, 1979a; Mills, 1990). When the carcass is big and fresh, they eat the viscera first, and then they cut through skin and flesh to separate all four legs from the body, in order to carry them for posterior consumption or storage. They eat considerably less in one sitting than spotted hyenas (an average of 5 kg of meat and 2 kg of bone or skin). When they feed at the den (in or out, there seems to be no preference), the bone accumulation always occurs in the same area (Owens and Owens, 1979a).

Aardwolves, finally, start eating when they find a colony of termites on the ground surface (Fig. 1.17). At the beginning, they mainly eat workers, but after a few minutes, soldiers become more abundant (as a result of workers being disturbed). Termite soldiers secrete noxious and tasteful terpenoids (Kruuk, 1972c; Anderson et al., 1992; Richardson and Levitan, 1994), which at some point prompt the aardwolf to stop eating and move toward the next colony. During all this process, a lot of debris and sand is consumed by the animal (Bothma, 1998).

Figure 1.17: Adult Aardwolf feeding on the surface in a zoo (Photo made by Josh More, 2014, CC BY-NC-ND 2.0, Flickr.com).

Defecation**.** Generally, the three larger hyenas defecate in delimitated latrines close to landmarks, because they also serve as scent-markers (Kruuk, 1976; Mills and Gorman, 1987). Interspecific differences in latrines are poorly documented; for example, those of brown hyenas are rather small and have a high feces concentration, whereas spotted hyenas use larger and less dense areas (Skinner and Van Aarde, 1981).

Aardwolves, in contrast, possess unique and characteristic defecation habits. In particular, they defecate in any of the middens located around their home range, with a maximum of four active middens per animal (although many more inactive areas may exist; Bothma, 1998). The middens are well-defined circles of ca. 1–2 m in diameter (Kruuk, 1972c), where they consequently accumulate feces, which have a characteristic terpene smell (Richardson, 1990). They are subsequently covered with sand and, usually, urinated on. These middens also serve as scent-makers, and when a midden is in the boundary between homeranges, both aardwolves cover the scent of each other continually (Nel and Bothma, 1983; Richardson, 1990).

Social Behavior

Despite their restricted extant diversity, hyaenids show a diverse array of social behaviors, ranging from extremely solitary to extraordinarily social (with complex behaviors in large societies), depending on the species. Spotted hyenas are gregarious and group into clans of up to 90 members, in which each individual plays a different role (Kruuk, 1972a; Mills, 1990; Henschel and Skinner, 1991). The remaining two species of larger hyenas are more solitary, and only form small groups, although the interaction between individuals and their social behaviors are rather complex (although less so than in spotted hyenas; Rieger, 1979; Mills, 1990). Aardwolves, in turn, are the most solitary species, being always alone, except when mating or taking care of cubs (Owens and Owens, 1979a; Richardson, 1991).

Grouping**.** Group formation patterns, as well as hierarchies and social organization within groups, are quite different between living hyaenid species, the most complex behaviors being displayed by spotted hyenas. They are summarized in order of increasing complexity, except for those of the aardwolf, which only pairs when mating (see section 'Reproduction and Life history' below).

Spotted hyenas always gather in huge clans (Kruuk, 1972a; Fig. 1.18), which basically consist in large fission-fusion matriarchal societies (Holekamp et al., 2000) that are divided into subgroups for resting and foraging (Kruuk, 1972a; Mills, 1990). These subdivisions make it hard

Figure 1.18: Several spotted hyenas, including cubs, gather around a communal den (Photo by Kate Nevens, 2008, CC BY-NC 2.0, Flickr.com).

for all the members of the clan to be found in the same place at the same time (Holekamp et al., 2000). Their hierarchical system is complex, with more than a single linear hierarchy ineach clan (Bertram, 1979), consisting of multiple matrilines of adult females with their offspring and surrounded by several immigrant males (Smith et al., 2008). Intersexual dominance hierarchies are found in both genders, but female hyenas dominate males (Frank, 1986b; Hofer and East, 1995). Normally, female hyenas are philopatric, i.e., they stay in their clan when they reach sexual maturity, further inheriting their mother's rank and creating stable dominance lines (Mills, 1990; Smale et al., 1997; East and Hoffer, 2001). The opposite occurs with males, which become nomads when they become sexually mature (Mills, 1990; Hoffer and East, 1995; East and Hofer, 2001), wandering and changing clans for some time until they establish permanently in a group (Frank, 1986b; Hofer and East, 1995). Subgrouping is rather complex because individuals decide which subgroup to join on the basis of its members (Szykman et al., 2001; Smith et al., 2007), being able to change their subgroup several times per day (Kolowski et al., 2007). In particular, they tend to join subgroups with kin (Holekamp et al., 1997; Wahaj et al., 2004), but also those that have potential mates and gender companions with slightly higher ranking (Szykman et al., 2001; Smith et al., 2007). The existence of subgroups, given this fission-fusion routine, allows spotted hyenas to respond better to ecological constraints (i.e., interspecies competiton), further enabling a more efficient usage of resources and a greater sociality (Smith et al., 2008). Depending on the region and habitat, the clans of spotted hyenas differ in number and minor subroutines. There is a clear difference between the clans of East and South Africa, basically due to differences in prey abundance (which is not a problem in

East Africa due to the prey/herbivore migratory patterns; Hofer and East, 1993a). In particular, clans in East Africa are formed by many individuals (up to 100 in the Ngorongoro Crater; Kruuk, 1966), whereas clans in South Africa are generally smaller; a minimum of 8 individuals per clan can be found in the central Namib Desert (Tilson and Henschel, 1986), although with some exceptions (Cooper, 1990a, b; 1991).

The social behavior of brown hyenas has been studied in depth, especially in the South Kalahari (Mills, 1990). They are not very social (Eaton, 1976), although tend to form smalls groups of related individuals and mixed genders (Owens and Owens, 1979a, b; Mills, 1982b, c). These groups can be formed by one or several females with their offsprings, while the males can inmigrate, remain in the clan or become nomadic when reaching adulthood (Owens and Owens, 1979a; Mills, 1990) These groups regionally differ in number and hierarchies (Owens and Owens, 1979a, b; Mills, 1990), due to differences in abundance, distribution, and food quality (Owens and Owens, 1979b; Mills, 1982a, 1983).

In striped hyenas, group formation also depends on several ecological factors, such as food abundance, resource availability, and competition (the latter one being the less important factor; Kruuk, 1976; Bouskila, 1984). Therefore, populations from different regions differ in how and when groups are formed. Generally, those from East Africa are solitary and have therefore developed behavioral adaptations for a solitary lifestyle. In contrast, striped hyenas from the Negev Desert form small groups of 2–4 individuals, due to decreased food availability (such that they have to form foraging groups in order to effectively forage; Bouskila, 1984). On a particular population from East Africa, it has been suggested that females and males form spatial “gender” groups in the area, instead of social or foraging groups (Wagner et al., 2008). According to this, the female group size might be determined only by food availability, whereas male groups would be determined by the number of males neighboring the female territories.

Communication. When communicating, hyenas use a variety of tactile, visual, vocal and olfactory systems. Vocalizations are quite common among carnivorans, being frequently used to maintain intergroup spacing and territory integrity (Hofer and East, 1995). Spotted hyenas have a wide range of different vocalizations, with up to 14 different types (Kruuk, 1972a; Henschel, 1986; Mills, 1990). The most common and recognizable one is the whooping (Kruuk, 1972a; Fig. 1.19), which they use for individual recognition (East and Hofer, 1991a, b; Holekamp, et al., 1999). This vocalization is not only used to defend the territory, but also to communicate between individuals (Hofer and East, 1995; Holekamp et al., 1999). Whoops are made by all individuals right after birth, being distinctive of each individual and consistent over time (East and Hofer, 1991a, b). Whoops are well studied (Kruuk, 1972a; Henschel, 1986; Mills, 1990; East and Hofer, 1991a, b; Theis et al., 2007), being divided into two types (slow vs. fast and highly pitched), with five different phases that are longer in slow whoops and shorter in the fast ones (Kruuk, 1972a; Henschel, 1986). Whoops can travel up to 5 km, and differ in tone and volume depending on the motivation, age and sex of the caller, although they generally communicate individual identity, age, positioning, motivational state and a request for support (Kruuk, 1972a; Mills, 1989, 1990; East and Hofer, 1991b; Bothma, 1998, Holekamp et al., 1999, 2007; Theis et al., 2007). Whoopings are used in different circumstances depending on the region; for example, in the Serengeti female hyenas use them when looking for aid in hard encounters with neighboring clans, when rallying the clan members, when trying to locate cubs, or when trying to defend communal resources (East and Hofer, 1991b; Bothma, 1998). In other areas, whoopings are used to identify and locate food resources (e.g., in theTimbavati Private Nature Reserve; Bearder, 1977) or convey mood and status to clan mates (e.g., in the Southern Kalahari Desert; Mills, 1990). Besides individual communication, the whooping system is vital for maintaining the complex social organization of hyena clans, with their ample range of vocalizations being in agreement with their varied and complex social behavior (Mills, 1990). In areas where clans are smaller (such as the Kalahari Desert), spotted hyenas have a much limited range of vocal displays; given that many clans only have a single adult male, male interaction is reduced to discourage nomad males, so a less complex “vocabulary” is required (East and Hofer, 1991a, b).

Figure 1.19: Spotted hyena whooping (Photo by Ramon, 2018, CC BY-NC 2.0, Flickr.com).

The vocalizations in the remaining three species of hyaenids, which lack the developed social skills of spotted hyenas, are less developed. Striped hyenas have a wide range of vocalizations, which have not been studied in depth but apparently resemble those of spotted hyenas (although being less varied, frequent and loud; Kruuk, 1976). Also, stripped hyenas vocalize much less in Africa than in Asia, to the point of being almost silent in east Africa, in order to avoid the dominant carnivores of the area (Kruuk, 1976). Brown hyenas have eight types of vocalizations (Mills, 1990), which they mainly use for short-range communications between individuals when foraging (although they can be heard from long distances; Owens and Owens, 1978; Mills, 1990). Aardwolves, finally, do not use vocalizations for individual communications.

With regard to olfactory communication, the most common type is scent marking, although the secreted scent is sometimes used differently in individual recognition, during aggressive encounters (Kruuk, 1972a; East et al., 1993; Burgener et al., 2008) or ritualized greeting ceremonies between members of the same clan of spotted hyenas (Kruuk, 1972a; East et al., 1993). Hyenas scent-mark in several ways, such as pasting, scratching, and using latrines, but unlike other carnivorans do not use urine for scent-making (Owens and Owens, 1978). Scent-marking in hyaenids has more than a single function, which vary between species (Bearder and Randall, 1978; Mills, 1990). Pasting is a scent-marking method exclusive of hyaenids (Kruuk, 1972b), consisting in paste gland anal strong-smelling secretions, produced in the anal pouch, onto objects in their range (Fig. 1.20; Mills, 1990). The anal pouch, located above the anus, is anatomically and histologically very similar in the four species, except for differences in shape (Flower, 1869; Murie, 1871; Pocock, 1916; Matthews, 1939; Kruuk and Sands, 1972; Mills et al., 1980; Macdonald, 1984; Mills, 1990; Sliwa, 1996; Stoeckelhuber et al., 2000). The pouch itself is formed by large amounts of sebaceous glands, with their external-most area being eversible and retractable. Brown hyenas and aardwolves produce two different kinds of pastes, due to the presence of secondary pasting areas in the former, and of a penile pad in the latter. In particular, next to the pouch, brown hyenas possess two circular and symmetrical areas that generate a second (dark) secretion (Murie 1871; Mills, 1990). In turn, the penile pad of the aardwolf (Flower, 1869; Sliwa, 1996) is only present in males, being located on the posterior surface of the penis (in front of the scrotum) and produces a dark and highly viscous secretion. Scratching consists in scent-mark objects with secretions from the interdigital glands (Kruuk, 1972a) and is complementary to pasting.

In spotted hyenas, scent-making patterns are varied. They scent-mark their territories well, marking the boundaries, the core areas, or important zones (depending on the region) with latrines (Gorman and Mills, 1984; Mills and Gorman, 1987; Henschel and Skinner, 1987), and pasting boundary intermediate points while patrolling (Henschel and Skinner, 1987). Brown hyenas similarly have many latrines across their territory, which are used as scent markers, being placed along the boundaries of the territory and next to clear landmarks (Mills, 1990). Striped hyenas also use latrines to mark certain areas of its range and paste within their territory, but not close to their den, unlike brown hyenas (Kruuk, 1976; Owens and Owens, 1979b). Aardwolves, in contrast, do not use their latrines as scent markers (Nel and Bothma, 1983).

Figure 1.20: Spotted hyena pasting (Photo by jennyshu47, 2013, CC BY-NC-ND 2.0, Flickr.com).

Pasting is individually recognizable in spotted and brown hyenas, which can certainly discriminate between individual pastes of their clan-mates (and, thus, recognize alien pasting; Mills, 1990; Burgener et al., 2008, 2009), whereas this feature has not been proven in striped hyenas or aardwolves. As said before, brown hyenas and aardwolves have two kinds of secretion: long-acting secretion (anal pouch) and short-acting secretion (secondary glands and penile pad, respectively). Brown hyenas use their second secretion, which is black and watery, as a marker for recent activity of a clan partner in that point (Mills and Gorman, 1987), e.g., after feeding of a renewable source to mark this spot as recently used and thus avoid unproductive foraging by other clan members. In aardwolves, the secondary secretion is not abundant and is used to recognize areas that have already been foraged that night (Nel and Bothma, 1983; Apps et al, 1989). The purpose of the primary long-acting secretion, in contrast, is quite similar in both species, being used for normal boundary and territory marking (Nel and Bothma, 1983; Gorman and Mills, 1984), as well as in the mating of aardwolves (Sliwa, 1996; Sliwa and Richardson, 1998).

When pasting and patrolling in groups, spotted hyenas spend a lot of time and resources, but the density of marked points and patrol routes vary within a single region as ecological conditions change (Henschel and Skinner, 1987; Mills and Gorman, 1987; Mills, 1990; Henschel and Skinner, 1991). The matriarchal system of spotted hyenas implies differences in the patrol composition: subadult males and females paste at equal rates, whereas adult males paste and patrol significantly more than adult females, and immigrant males paste more than long-established males (Mills and Gorman, 1987; Mills 1990; Burgener et al., 2008). The pasting rate further increases as they get far from the inner core or along the periphery of their territory (Mills and Gorman, 1987). Pasting is the main scent-marker for brown hyenas as well, being by far more regularly made than in spotted hyenas (Mills, 1990). Despite the higher pasting rates of the brown hyenas, their small clan numbers and vast territories make the long-acting pasting vital, as it allows a few individuals to properly scent-mark their territorial boundaries or even their whole territory (Gorman and Mills, 1984; Mills, 1990). For striped hyenas, pasting is based on a single type of secretion as in spotted hyenas, although the time spent in pasting and scent-marking is intermediate the spotted and brown hyenas (Kruuk, 1976; Owens and Owens, 1979b). Aardwolves paste along the boundaries of their territory, but the density of marks depends on the size of it: large areas are hard to monitorize, and thus, the density of the markers is low, but as counterpart, the message within the pasting is more intense (Richardson, 1991; Sliwa, 1996; Sliwa and Richardson, 1998). They generally scent on grass stalks only within their territory, but this is severely altered during the mating period (Richardson, 1991; Sliwa, 1996; Sliwa and Richardson, 1998). Male aardwolves tend to be more along the boundaries, as they spend more time defending the territory from neighboring males, whereas females remain in the center of the territories (Richardson, 1990 Sliwa, 1996; Sliwa and Richardson, 1998). Aardwolves usually enter and paste into neighboring territories during the winter mating seasons to initiate the frequently observed extrapair copulations (Richardson, 1987a; Sliwa 1996).

Reproduction and life history

Although three out of four of the extant species of hyenas display the normal reproductory systems of carnivorans, with males and females clearly differentiated, in the spotted hyena females and males possess similar external features in their reproductive organs. In particular, female spotted hyenas have a peniform and erectile clitoris, as well as a false scrotum (Mathews, 1939; Deane, 1962; Racey and Skinner, 1979; Van Jaarsveld and Skinner, 1987). The cause behind this unique feature can be related to high fetal androgen levels, which produce an overdevelopment of the sexual organs in females during their embryonic development. These high levels of androgens are also related to the previously discussed dominance and aggressions on the males (Van Jaarsveld and Skinner, 1987).

Hyenas reach sexual maturity at about 2–3 years of age, although this somewhat differs depending on the species. The three larger species are polyestrous (i.e., they have more than a single estrus per year; Rieger, 1979; Bothma, 1998), with reproductive periods occurring throughout the whole year and depending on resource availability. Aardwolves, in contrast, have a single estrus per year, commonly during the winter (Richardson, 1987c). Mating systems are interspecifically diverse. Male spotted hyenas can only mate when they are dominant in their clan, although all the males can court females, making their mating process highly polygynous (Kruuk, 1972a; East and Hofer, 2001; East et al., 2003). Mating in the smaller brown hyena clans takes place between resident clan females and nomad or immigrant males (Mills, 1982c, 1990; Owens and Owens, 1984), and generally only a single female per clan gives birth to cubs each year, thereby creating some competition for breeding (Owens and Owens, 1984). The stripped hyena males mate by following an estrous female for days, but it has only been observed in captivity (Bothma and Walker, 2013). The purportedly monogamous aardwolf surprisingly displays cuckoldry as a common trait, being otherwise known among some birds and primates. Close to the star of the female's sexual cycle, neighbor males paste and visit the female, while the resident male is out (probably doing the same), so that, when the time comes the resident male is not the only one that has copulated with the female (Bothma, 1998). This leads into sperm competition and dubious insemination, and although the resident male will take care of the litter notwithstanding, overall it results in sexual promiscuity despite a monogamous sociosexual organization (Richardson, 1987c).

Figure 1.21: Aardwolf cubs (photo by Wildlife Wonderer, 2017, CC BY-NC-ND 2.0, Flickr.com).

Gestation time is also variable between hyaenid species (Eaton, 1976; Rieger, 1979; Van Jaarsveld et al., 1988; Frank et al., 1995; Bothma, 1998). The longest gestation is that of the spotted hyena (110 days; Mathews, 1939), followed by that of striped and brown hyenas (90 days; Pocock, 1941; Skinner, 1976), and finally that of aardwolf (60 days). With regard to litter size, they greatly differ between species (Eaton, 1976; Owens and Owens, 1984; Mills, 1990; Bothma, 1998): spotted hyenas have 1–3 cubs (mean of 1.7; Holekamp and Smale, 1995; Hofer and East, 1997, 2008), striped and brown hyenas 1–5 cubs (means of 2.4 and 2.3, respectively; Skinner, 1976; Skinner and Ilani, 1979) and aardwolves have 1–4 cubs (average not reported). In general, hyenas are born with the eyes closed (except for the spotted hyena; Pournelle, 1965; Rieger, 1981; East et al., 1989), not being opened until several days later (Schultz, 1966; Bothma, 1998). Cubs (Fig. 1.21) are located, at least during the first days, at the natal dens, normally with a single litter per den (except in spotted hyenas, in which multiple litters can share a single den; Mills, 1990). These natal dens, which provide shelter during the first stages of postnatal development, basically consist in a borrow, a small cave, a cavity, or a clump of bushes (Eaton, 1976; Bothma, 1998); however, in spotted hyenas they are a little bit more complex, consisting of an entrance followed by a small and narrow tunnel (only accessible by the cubs) that leads to a bigger chamber (Bothma, 1998). The cubs start to venture out after a few days, ten in striped hyenas, whereas in spotted hyenas they are transferred to the communal dens after only two weeks (Mills, 1990; Bothma, 1998). Brown hyenas, in contrast, do not move their cubs to the communal den until 2–3 months after birth (Owens and Owens, 1984). Finally, aardwolf cubs stay within the den for the first three months, although these dens are changed regularly (Richardson, 1987c). Spotted hyenas suckle for 14–18 months (East and Hofer, 1991), which is similar to the lactancy periods of striped and brown hyenas (generally 10–12 months), whereas aardwolves only suckle for 5 months (Richardson, 1987c). This may vary in locally as in the Southern Kalahari brown hyenas only suckle for three months. Allosuckling is common in the communal dens of brown hyenas (as the mothers are usually out foraging or patrolling for long periods; Owens and Owens, 1984; Knight et al., 1992), and it has been also reported for spotted hyenas in some areas (Mills, 1990) despite claims of the contrary (Cooper, 1993). Although weaning time is rather late, all hyenas start eating their respective normal diets much earlier. Spotted hyena females usually do not carry food to their dens for the cubs, which start their carnivorour diet a little later than the other species, although sporadically they can access bones and other remains that other adult hyenas carry to the den (Mills and Mills, 1977; Hill, 1980; Skinner et al., 1986; Mills, 1989). Striped and brown hyenas, in turn, normally carry meat or carcasses to their cubs in the den, but neither of them regurgitates food (Owens and Owens, 1979b; Bothma, 1998); the cubs start to eat meat after 30 days in striped hyenas (Rieger, 1979) and 95 days in brown hyenas (Mills, 1989). Due to the dietary habits of the aardwolf, the parents cannot bring food to the den, so that the cubs do not start eating termites directly from the patch until they go out of the den, which occurs at about three months of age (Richardson, 1979c).

Parental caring is quite different in each hyaenid species. In spotted hyenas, it largely depends on litter size, habitat size, and the clan itself. The time of attention that one cub needs is much lesser than that spent in twins, making single cub growing and surviving rates higher as compared to twins (Hofer and East, 1993b, 2003, 2008; Bothma, 1998). At the den, the mother visits twice a day her cubs, and actively defends them during the first four weeks, subsequently visiting them less often (Bothma, 1998). Coupled with the long trips that are sometimes required by the mother to forage, this may result in long time spans during which the cubs are not fed and lose weight (Hofer and East, 1993b). Minor differences may occur due to ecological changes. For example, in the Kruger National Park seasonal food abundance impacts in the mother's ability to produce milk (Henschel and Skinner, 1987), whereas the low amount of resources in the Kalahari and the long distances that the mother has to travel make allosuckling necessary in this area (Mills, 1990); in the Savuti Marsh, the cubs are taken to the den during the night and are guarded by a couple of adults while the rest of the clan is hunting

(Cooper, 1993). Spotted hyena cubs inherit their mother's hierarchical status, so that male cubs of dominant females tend to be more aggressive and show less submission to dominant females when compared to cubs of non-dominant females (East et al., 1993; Holekamp and Smale, 1993), sometimes even leading to severe fights between different male cubs that may lead to the death of one of the siblings (Werdelin and Solounias, 1991). Generally, brown hyena females provide food to the cubs of their clan without considering rank or relatedness (Owens and Owens, 1979b), in contrast to males, which only provide food to half-sibling cubs (Mills, 1990; Bothma, 1998). Brown hyenas further provide parental care for their clan's cubs at the communal den, as adults forage far from it, being absent for long periods of time (Owens and Owens, 1979b). Striped hyena cubs are frequently visited by their mother for sucking or carrying food (Kruuk, 1976; Skinner and Ilani, 1979; Davidar, 1990). Due to the diet of the aardwolf, the only function of the male in parental care consists of intense den defense; they only forage during 3 hours, when females are in the den with the cubs, and otherwise guard it when the female goes out for food during the whole night (females require more intense feeding due to lactancy; Richardson, 1987c).

Figure 1.22: Spotted hyena cubs emerging from a communal den (Photo by MudflapDC, 2017, CC BY-NC-ND 2.0, Flickr.com).

The cubs (Fig. 1.22) leave the communal den when they are older. In spotted hyenas, they leave after a year (Hofer and East, 1993a; Frank et al., 1995). Once they are subadult, males have to become nomads or migrate to another clan, whereas females can remain and inherit their mother's position (Frank, 1986b: Höner et al., 2010). This may vary locally, as in the Kalahari males can remain in the clan, and females can migrate or establish a new clan (Mills, 1990). Brown hyenas leave the den at 10 months as subadults and start to forage alone, but tend to return to the den until they become sexually active (around 30 months; Mills, 1982d, 1990); at this point, they may remain in the group or migrate to another one (Mills, 1982c; 1983). The other two species simply migrate from their parents' clan as nomads, in the case of the striped hyena, or to find a mating couple in the case of the aardwolf (Rieger, 1979; Richardson, 1987c).

Competition

In general terms, hyenas don't overlap in the diet with other carnivorans, due to size, habitat and hunting behaviors (Fig. 1,23). This lets the interspecies relationships more focused in practical interference than in real competition, as only one of the four species actively hunts.

Figure 1.23: A brown hyena steals the prey to young cheetahs in the kalahari (Photo by Derek Keats, 2017, CC BY 2.0, Flickr.com).

Competition between hyaenids. The interaction between different species of hyenas depends on diet and distribution. This is exemplified by the low interaction between brown and striped hyenas (due to their minor distribution overlap) or by the low interaction between the aardwolf and other hyaenids (due to their entirely different dietary habits). The major competition among extant hyaenids is between brown and spotted hyenas, in areas where the former is abundant, and mainly regarding the use of carrion. The distribution of brown and spotted hyenas in the overlapping areas is distinct because the former tend to avoid the latter. For example, in the Kalahari Gemsbok National Park, almost all brown hyena dens are located in dune areas (93%), whereas a majority of spotted hyena dens are situated in the riverbeds (69%; Mills and Mills, 1982). The exclusively nocturnal habits of the former further promote the lack of contact between the two species (Mills, 1977). In areas where striped and spotted hyenas overlap, there is competition for carrion, as in the case of brown hyenas, although the former tend to avoid contact with large predators, thereby maintaining their interaction low.

Competition with other carnivorans. The competition of spotted hyenas with other carnivores is variable depending on the area; for example, it is higher in the Ngorongoro than in the Serengeti (Kruuk, 1970). Furthermore, the species with whom they interact are different, depending on the abundance of other predators; for example, cheetahs and painted dogs are much more abundant in the Umfolozi Game reserve than in the Timbavati Private Nature Park, thereby resulting in a higher interaction with spotted hyenas in the former (Bearder, 1977; Skinner et al., 1992).

Lions (Fig. 1.24) are one of the major competitors of spotted hyenas, given that they generally kill the same kind of medium-sized preys. Depending on the prey and region, the extent of this competition also varies. Thus, lions tend to kill subadult gemsbok and wildebeest in the Southern Kalahari, whereas spotted hyenas kill calves, lowering or avoiding the competition in that region; in contrast, when both species have to kill adult gemsbok, the lions tend to win and deny that resource to hyenas. Mutual prey robbery is common between these species in some areas of East Africa and in the Savuti, whereas in other regions, such as the Southern Kalahari, hyenas and lions wait until the other species finishes with the prey to move in, thereby avoiding major conflicts. Competition in the Savuti is higher because large groups of spotted hyenas can displace groups of lions if the latter do not include a male (as hyenas avoid such confrontation); in contrast, up to 25% of the kills made by spotted hyenas are stolen by male lions (Cooper, 1990a). Solitary lions cannot succeed against a group of hyenas (Mills, 1990), so that the competition with hyenas has promoted the development of hunting strategies by lions (Macdonald, 1983).

Figure 1.24: Spotted hyenas trying to take over a carcass from lions in the Ngorongoro (Photo by Megan Coughlin, 2013, CC BY-ND 2.0, Flickr.com).

Competition between hyenas and smaller carnivorans is more restricted, but similarly variable regionally (Bothma, 1998). In case of conflict, a single spotted hyena can usually dominate a leopard, a cheetah, a jackal and a wild dog. Although leopards and hyenas do not interfere or compete when hunting (due to the smaller preys hunted by leopards), spotted hyenas tend to harass and dominate leopards due to their number superiority (as leopards are solitary) when faced. Such interactions do not always involve food, but when they do, leopards can hide the prey up in a tree, where hyenas cannot reach it, so that the amount of food that hyenas steal from leopard is relatively restricted (Mills, 1990). The same applies between spotted hyenas and cheetahs, due to the lack of overlapping prey selection and the similarly low rates of food stealing (Mills, 1990). There is no interaction between caracals and spotted hyenas (Mills, 1990, and the interaction with black-backed jackals is also small, although the latter sometimes deprive food for the hyenas or scavenge hyena kills (Mills, 1990).

In general terms, brown hyenas rank lower than spotted hyenas in the predator hierarchy, being only able to subjugate cheetahs when they are alone (Eaton, 1976; Mills, 1990). Their interaction with lions, although scarce due to the low population of lions where brown hyenas inhabit (Mills, 1990), normally ends badly for brown hyenas, as lions sometimes chase and hunt them down, or mutilate them for no apparent reason (Owens and Owens, 1979b; Eloff, 1984; Mills, 1990). Despite these facts, lion kills are one of the primary food sources for brown hyenas, although the latter feed upon them only after lions leave the prey. In contrast, lions rarely try to drive away brown hyenas from carcasses, especially those not killed by predation (Mills, 1990).

Although brown hyenas can sometimes steal a prey from a leopard, the ability of the latter to place them up a tree precludes brown hyenas from scavenging the carcass (Mills, 1990), resulting in an overall low interaction between both species. Cheetahs, in contrast, do provide brown hyenas with carcasses, which are consumed by brown hyenas at night when the cheetah has already left. This makes the interaction between them low, except for some occasions when a brown hyena chases a cheetah with a prey killed close to nightfall (Mills, 1990). The major interaction comes with black-backed jackals, as they scavenge food and prey on animals of the same size. Brown hyenas will only harass black-backed jackals is there is food at stake, but they have been seen commonly scavenging together in carcasses. The fact that jackals cannot break bones gives the hyenas an advantage, which compensates for the food deprived by the jackals, resulting in an overall balanced competition (Mills, 1990).

The main competitor (and major threat) of striped hyenas are humans, especially in Asia, because many parts of their body have superstitious, medical or aphrodisiac usages in many areas (Bothma, 1998). Generally, striped hyenas do not interact with large predators, whereas smaller predators are either ignored or predated by them (Kruuk, 1976).

Aardwolves only go into direct dietary competition with three other carnivorans (Richardson, 1987a, b): the bat-eared fox, the Cape fox, and the black-backed jackal (Bothma, 1998). The two latter have a wide and varied diet that is not focused on termites, thus making their competition with aardwolves quite small (Bothma, 1998). Competition between these species if further restricted due to the avoidance of short grass habitats by the Cape fox or the low time spent by black-backed jackals on termite patches. There is a much higher dietary overlap with the bat-eared fox (Bothma et al., 1984), which nevertheless eats a higher variety of insects. Differences in foraging habits, and the fact that neither of these species increase the variety of foods consumed in moments of environmental stress (such as droughts), suggest that there is plenty of resources for both of them. All the above considerations make the coexistence of these four species plausible within a single area (Bothma et al., 1984).

1.2. Extinct hyaenids

The diversity and geographic distribution of hyaenids was much greater in the past, with more than 60 taxonomically valid species known from the fossil record (Turner et al., 2008). These are distributed throughout Africa, Eurasia and, punctually, even North America (Werdelin and Solounias, 1991; Turner et al., 2008). Hyaenids are first recorded in Europe by the middle Miocene (MN4, ca. 16 Ma; Ginsburg and Bulot, 1982; Werdelin and Solounias, 1996).

1.2.1. Systematics and phylogeny

Systematics

The systematics of hyaenids has been a mess until a few decades ago, when Werdelin and Solounias (1991) organized all the known genera (both extant and extinct) into three subfamilies (Hyaeninae, Protelinae and Ictitheriinae), after extensively reviewing most of the available material. Subsequent authors have followed this work, although there are still some ongoing debates.

Earliest discussions revolved around the lack of consensus about what is a hyaenid. The first and most consistent diagnosis was given by Winge (1895), being based on the characteristics of the bulla. Previous authors (e.g., Gaudry, 1873), in contrast, had tried to separate viverrids from hyaenids on the basis of the dentition, by considering the loss of the M2 as a synapomorphy of the latter group. In the mid 19th century, both living and extinct hyaenids were included in a single genus, *Hyaena*; except for *Proteles*, which was not considered a hyaenid yet (See section 1.1.1; Roth and Wagner, 1854; Von Nordmann, 1858; Gaudry, 1861, 1862-1867; Gervais, 1846, 1850, 1859). This consensus was slightly altered by the erection of two extinct genera, *Hyaenictis* Gaudry, 1861 and *Lycyaena* Hensel, 1862. Subsequent works further described new genera and species as new finds accumulated, but a major restructuring of hyaenid systematics at the genus rank did not occur until Kretzoi (1938), who erected many extinct genera still considered valid nowadays, such as *Plioviverrops* Kretzoi, 1938, *Hyaenictitherium* Kretzoi, 1938 and *Pachycrocuta* Kretzoi, 1938. For the next four decades, several major works (Villalta Comella and Crusafont Pairó, 1943, 1945; Crusafont Pairó and Petter, 1969; de Beaumont and Mein, 1972; Hendey, 1974; Kurtén, 1976; Schmidt-Kittler, 1976) expanded the number of hyaenid species known from the fossil record, but it was not until the 1980s when these works began to be reviewed and summarized by a series of studies focused on different lineages and particular genera (e.g., Howell and Petter, 1980, 1985; Qiu, 1987; Werdelin, 1988a, b; Semenov, 1989; Werdelin and Solounias, 1990), leading to the revision (including the synonymization) of the species within some genera, such as *Adcrocuta* Kretzoi, 1938, *Hyaenictitherium*, *Chasmaporthetes* Hay, 1921, *Pachycrocuta*, etc. Slightly later, Werdelin and Solounias (1991) provided a detailed summary of the available data for extinct hyaenids, including many synonymies. Later works further clarified some of the still unsolved issues (de Bonis and Koufos, 1994; Werdelin et al., 1994; Werdelin and Turner, 1996b; Werdelin, 1999; Werdelin and Kurtén, 1999), such as the taxonomic attribution of some specimens from Langenbaanweg (Werdelin et al., 1994). Recently, some specific works have been published to update the available data on extinct hyaenids from some regions (Turner et al., 2008; Werdelin and Peigné, 2010; Koufos, 2011). Currently, the most hotly debated topic in hyaenid taxonomy and systematics probably regards the genera *Hyaenotherium* Semenov, 1989 and *Hyaenictitherium* (see Semenov, 1989, 2008; Werdelin and Solounias, 1991; Koufos, 2000; Zhang et al., 2002; de Bonis, 2004, 2005; Andersson and Werdelin, 2005; Tseng and Wang, 2007; Koufos, 2009).

Nowadays the family Hyaenidae includes 3 subfamilies and 24 genera, following to Turner et al. (2008). The complete taxonomy of extant and extinct hyaenids is reported in Table 1.2.

Tabla 1.2 (next page): Complete taxonomy of the family Hyaenidae family, including both extant and extinct species (the latter are denoted by a dagger). In spite of the current debate, the genus *Hyaenotherium* is considered a junior synonym of *Hyaenictitherium*, due to the lack of arguments supporting a clear distinction between the two forms (Zhang et al., 2002; Andersson and Werdelin, 2005; de Bonis, 2004, 2005; Koufos 2011)

Family **Hyaenidae** Gray, 1821
- †Subfamily **Ictitheriinae** (Trouessart, 1897)
  - †Genus *Protictitherium* Kretzoi, 1938
    - †*Protictitherium crassum* (Depéret, 1892)
    - †*Protictitherium gaillardi* (Forsyth Major, 1903)
    - †*Protictitherium cingulatum* Schmidt-Kittler, 1976
    - †*Protictitherium intermedium* Schmidt-Kittler, 1976
    - †*Protictitherium llopisi* (Crusafont Pairó & Petter, 1969)
    - †*Protictitherium punicum* (Kurtén, 1976)
    - †*Protictitherium sumegense* Kretzoi, 1984
    - †*Protictitherium csakvarense* Kretzoi, 1951
  - †Genus *Plioviverrops* Kretzoi, 1938
    - †*Plioviverrops gervaisi* de Beaumont & Mein, 1972
    - †*Plioviverrops orbignyi* (Gaudry & Lartet, 1856)
    - †*Plioviverrops faventinus* Torre, 1989
    - †*Plioviverrops guerini* (Villalta Comella & Crusafont Pairó, 1945)
    - †*Plioviverrops gaudryi* de Beaumont & Mein, 1972
  - †Genus *Tunguricti*s Colbert, 1939
    - †*Tunguricti*s *spocki* Colbert, 1939
  - †Genus *Thalassictis* Gervais, 1850 ex Von Nordmann ms.
    - †*Thalassictis robusta* Gervais, 1850 ex Von Nordmann ms.
    - †*Thalassictis certa* (Forsyth Major, 1903)
    - †*Thalassictis montadai* (Villalta Comella & Crusafont Pairó, 1943)
    - †*Thalassictis proava* (Pilgrim, 1910)
    - †*Thalassictis sarmatica* (Pavlow, 1908)
    - †*Thalassictis spelaea* (Semenov, 1988)
  - †Genus *Tongxinictis* Werdelin & Solounias, 1991
    - †*Tongxinictis primordialis* (Qiu et al., 1988a)
  - †Genus *Ictitherium* Wagner, 1848
    - †*Ictitherium viverrinum* Roth & Wagner, 1854
    - †*Ictitherium tauricum* Borissiak, 1915
    - †*Ictitherium ibericum* Melazde, 1967
    - †*Ictitherium kurteni* Werdelin, 1988
    - †*Ictitherium intuberculatum* Ozansoy, 1965
    - †*Ictitherium pannonicum* Kretzoi, 1952
  - †Genus *Miohyaenotherium* Semenov, 1989
    - †*Miohyaenotherium bessarabicum* Semenov, 1989
  - †Genus *Hyaenictitherium* Kretzoi, 1938
    - †*Hyaenictitherium wongii* (Zdansky, 1924)
    - †*Hyaenictitherium hyaenoides* (Zdansky, 1924)
    - †*Hyaenictitherium parvum* (Khomenko, 1914)
    - †*Hyaenictitherium pilgrimi* Werdelin & Solounias, 1991
    - †*Hyaenictitherium namaquensis* (Stromer, 1931)

†*Hyaenictitherium minimum* de Bonis et al., 2005
†*Hyaenictitherium wongii* (Zdansky, 1924)
†*Hyaenictitherium ebu* (Werdelin, 2003)
Subfamily **Protelinae** (Geoffroy Saint-Hilaire, 1851)
Genus *Proteles* Geoffroy Saint-Hilaire, 1824
Proteles cristata (Sparrman, 1783)
†*Proteles amplidentus* Werdelin & Solounias, 1991
Subfamily **Hyaeninae** (Gray, 1821)
†Genus *Lycyaena* Hensel, 1862
†*Lycyaena chaeretis* (Gaudry, 1861)
†*Lycyaena dubia* Zdansky, 1924
†*Lycyaena macrostoma* (Lydekker, 1884)
†*Lycyaena crusafonti* Kurtén, 1976
†Genus *Hyaenictis* Gaudry, 1861
†*Hyaenictis graeca* Gaudry, 1861
†*Hyaenictis almerai* Villalta Comella & Crusafont Pairó, 1945
†*Hyaenictis hendeyi* Werdelin et al., 1994
†*?Hyaenictis wehaietu* Haile-Selassie and Howell 2009
†Genus *Lycyaenops* Kretzoi, 1938
†*Lycyaenops rhomboidea* Kretzoi, 1938
†*Lycyaenops silberbergi* (Broom in Broom and Schepers, 1946)
†Genus *Chasmaporthetes* Hay, 1921
†*Chasmaporthetes exitelus* Kurtén and Werdelin 1988
†*Chasmaporthetes bonisi* (Koufos, 1987)
†*Chasmaporthetes borissiaki* (Khomenko, 1932)
†*Chasmaporthetes lunensis* (Del Campana, 1914)
†*Chasmaporthetes melei* Rook et al., 2004
†*Chasmaporthetes ossifragus* Hay, 1921
†*Chasmaporthetes australis* (Hendey, 1974)
†*Chasmaporthetes nitiluda* (Ewer, 1955)
†*Chasmaporthetes gangsrienrsis* Tseng et al., 2013
†Genus *Metahyaena* Viranta and Werdelin, 2003
†*Metahyaena confector* Viranta and Werdelin, 2003
†Genus *Palinhyaena* Qiu et al., 1979
†*Palinhyaena reperta* Qiu et al., 1979
†Genus *Belbus* Werdelin and Solounias, 1991
†*Belbus beaumonti* (Qiu, 1987)
†Genus *Allohyaena* Kretzoi, 1938
†*Allohyaena kadici* Kretzoi, 1938
†Genus *Adcrocuta* Kretzoi, 1938
†*Adcrocuta eximia* (Roth and Wagner, 1854)
†Genus *Pliocrocuta* Kretzoi, 1938
†*Pliocrocuta perrieri* (Croizet and Jobert, 1828)
†Genus *Pachycrocuta* Kretzoi, 1938
†*Pachycrocuta brevirostris* (Gervais, 1850)

- †Genus *Ikelohyaena* Werdelin and Solounias, 1991
    - †*Ikelohyaena abronia* (Hendey, 1974)
- Genus *Hyaena* Brisson, 1762
    - *Hyaena hyaena* (Linnaeus, 1758)
    - †*Hyaena makapani* Toerien, 1952
- Genus *Parahyaena* Hendey, 1974
    - †*Parahyaena howelli* Werdelin, 2003
    - *Parahyaena brunnea* (Thunberg, 1820)
- Genus *Crocuta* Kaup, 1828
    - *Crocuta crocuta* (Erxleben, 1777)
    - †*Crocuta spelaea* (Goldfuss, 1823)
    - †*Crocuta dietrechi* Petter and Howell, 1989
    - †*Crocuta eturono* Werdelin and Lewis, 2008

Phylogeny

Hyaenid phylogeny has been a matter of intense debate during the last 150 years. During the 19th century and a large portion of the 20th century, works focusing on hyaenid interrelationships were not common (e.g., Roth and Wagner, 1854; Von Nordmann, 1858; Lydekker, 1884; Kretzoi, 1938) and only a fewer number depicted clearly their ideas about the whole family (e.g., Gaudry, 1862-1867; Schlosser, 1890; Pilgrim, 1932; Kretzoi, 1938; Thenius, 1966; Fig 1.25). The first cladistic analysis came to aid in this topic in the last quarter of the 20th century (Galiano and Frailey, 1977), and the detailed work by Werdelin and Solounias (1991) established the basis for the currently accepted hyaenid phylogeny, even though significant improvements and extensions followed in later works (Werdelin and Solounias, 1996; Werdelin and Turner, 1996b; Ferretti, 1999; Turner et al., 2008; Tseng al., 2011; Fraile, 2015).

The historically hottest debate concerning the phylogeny of hyaenids concerns the relationships between *Hyaena*, *Parahyaena* and *Crocuta* (Gaudry 1862-1867; Schlosser, 1890; Pilgrim, 1932; Ewer, 1955; Thenius, 1966; Hendey, 1974; Galiano and Frailey, 1977; Werdelin and Solounias, 1991). This was not conclusively resolved until molecular analyses favored the hypothesis that *Hyaena* and *Parahyaena* are more closely related to one another than to *Crocuta* (Jenks and Werdelin, 1998; Koepfli et al., 2006). Another noteworthy debate, which concerns the concept of hyaenid itself, is the inclusion/exclusion of the Ictitheriinae within/from the Hyaenidae. Initially, they were included within the Viverridae (Roth and Wagner, 1854; Von Nordmann, 1858; Gaudry, 1861, 1862-1867; Gervais, 1846, 1850, 1859), but Lydekker (1884) suggested their inclusion in the family shortly before Winge's (1895) definition of the Hyaenidae, when their belonging to the Viverridae was still accepted (Schlosser, 1890). Later authors (Pilgrim, 1931, 1932; Thenius, 1966) followed Winge's definition and included these ictitheriine genera in the Hyaenidae. This next debate in hyaenid systematics related to the percrocutids, which at some point were included within the Hyaenidae (Pilgrim, 1931, 1932; Thenius, 1966), but subsequently excluded (with the exception of *Adcrocuta*) based on detailed analyses (Ficarelli and Torre, 1970; Hendey, 1974; Schmidt-Kittler, 1976; Guanfang and Schmidt-Kittler, 1983; Qiu et al., 1988b) that supported a different origin based on the deciduous dentition and some cranial characters. The main argument relied on the more derived features of the dP4 in percrocutids as compared to hyaenids (Schmidt-Kittler, 1976; Guanfang and Schmidt-Kittler, 1983). The distinction between the two groups was further supported by cranial characters from the basicranium and the tympanic bullae (Qiu et al., 1988b), as well as by the frontal placement of the orbit in percrocutids (Werdelin and Solounias, 1997).

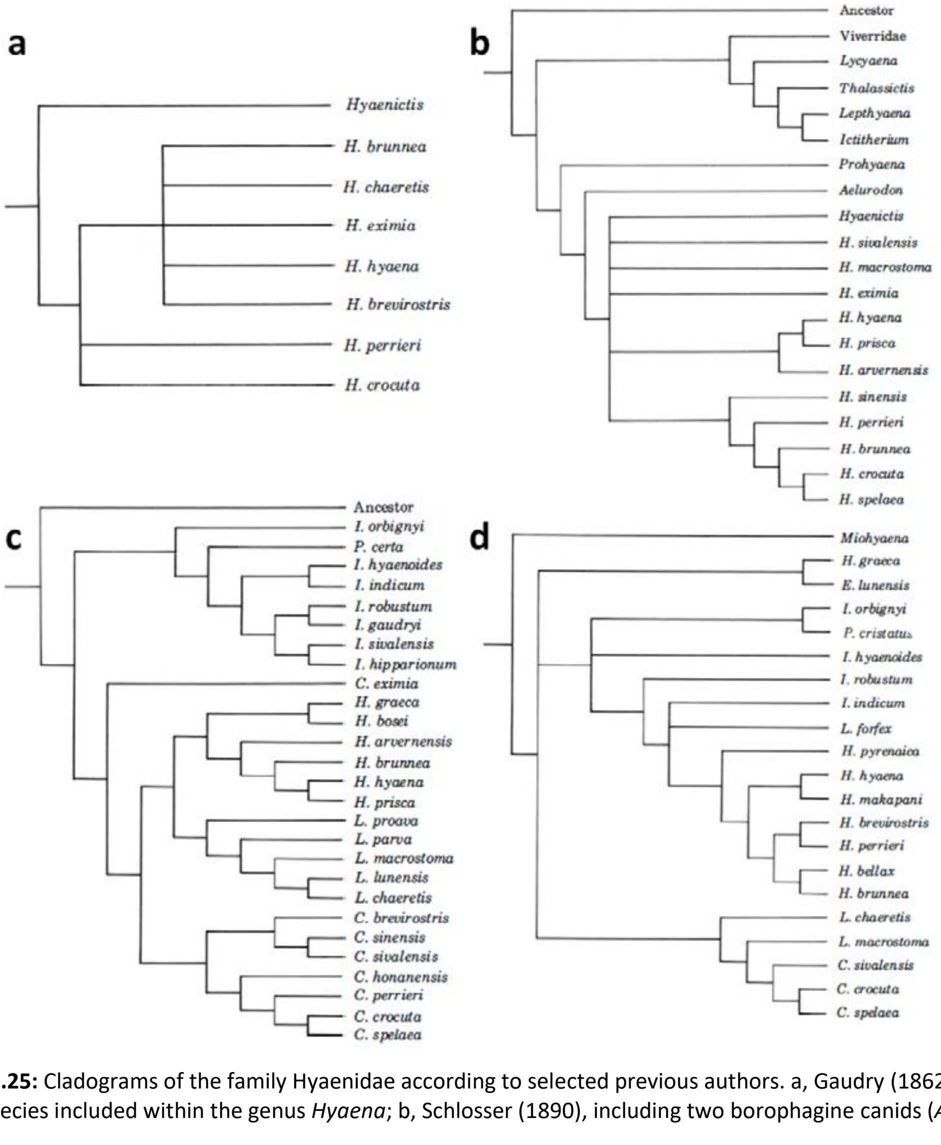

Figure 1.25: Cladograms of the family Hyaenidae according to selected previous authors. a, Gaudry (1862-1867), with all species included within the genus *Hyaena*; b, Schlosser (1890), including two borophagine canids (*Aelurodon*

and *Prohyaena*) that were formerly considered hyenids; c, Pilgrim (1932); d, Thenius, (1966). Figure modified from Werdelin and Solounias (1991).

Other issues related to the internal phylogeny of the Hyaenidae have been discussed in the literature, such as the phylogenetic origins of the family. Before the inclusion of ictitheriines into the Hyaenidae, viverrids where considered as broadly ancestral to the group, with being *Hyaenictis* the basal-most form (e.g., Gaudry 1862-1867; Schlosser, 1890). After the inclusion of the ictitheriines, viverrids or herpestids were still considered ancestral to hyaenids by some authors (de Beaumont, 1967, 1968, 1969b), but the doubt remained about hyaenid monophyly. A possible diphyletic origin was suggested by some authors (Kretzoi, 1938; Crusafont-Pairó and Petter, 1969), who even considered the creation of two distinct families. In contrast, hyaenid monophyly was supported by most other authors (Abu Bakr, 1959; Ficarelli and Torre, 1970; Hendey, 1974; Schmidt-Kittler, 1976), who favored a scenario where the more derived hyenas evolved from *Ictitherium* and other basal forms, such as *Protictitherium* or *Thalassictis*. Other important ideas put forward in the above-cited works include: the evolution of *Chasmaporthetes* from *Lycyaena* and *Hyaena* from *Ictitherium*, thereby outlining the two markedly distinct evolutionary pathways accepted nowadays, durophagy and hypercarnivory, followed by members of the family since late Miocene (Ficarelli and Torre, 1970); the consideration of some African species, such as *Ikelohyaena abronia*, as direct ancestors of the extant bone-crackers (Hendey, 1974); and the idea that extant bone-crackers form a monophyletic clade with the Plio-Pleistocene genera *Pliocrocuta* and *Pachycrocuta* (Galiano and Frailey, 1977).

As explained above, the work by Werdelin and Solounias (1991) organized all the then available data, and the inclusion of a cladistic analysis settled many of the previous debates. With this stable base to work on, the latter works focused more on increase the resolution, support, or simply update the phylogeny (e.g., Werdelin and Solounias, 1996; Werdelin and Turner, 1996b; Jenks and Werdelin, 1998; Koepfli et al., 2006; Ferretti, 2007; Turner et al., 2008; Sheng et al., 2014; Fraile, 2015). No new cladistic analysis (i.e., based on different characters) has been subsequently published to date, its several refinements notwithstanding. One of these (Werdelin and Solounias, 1996) is especially important, as it proposes several hypotheses about the ancestors of each lineage (Fig 1.26), with *Hyaenictitherium* being the most likely ancestor of the bone-cracking hyenas.

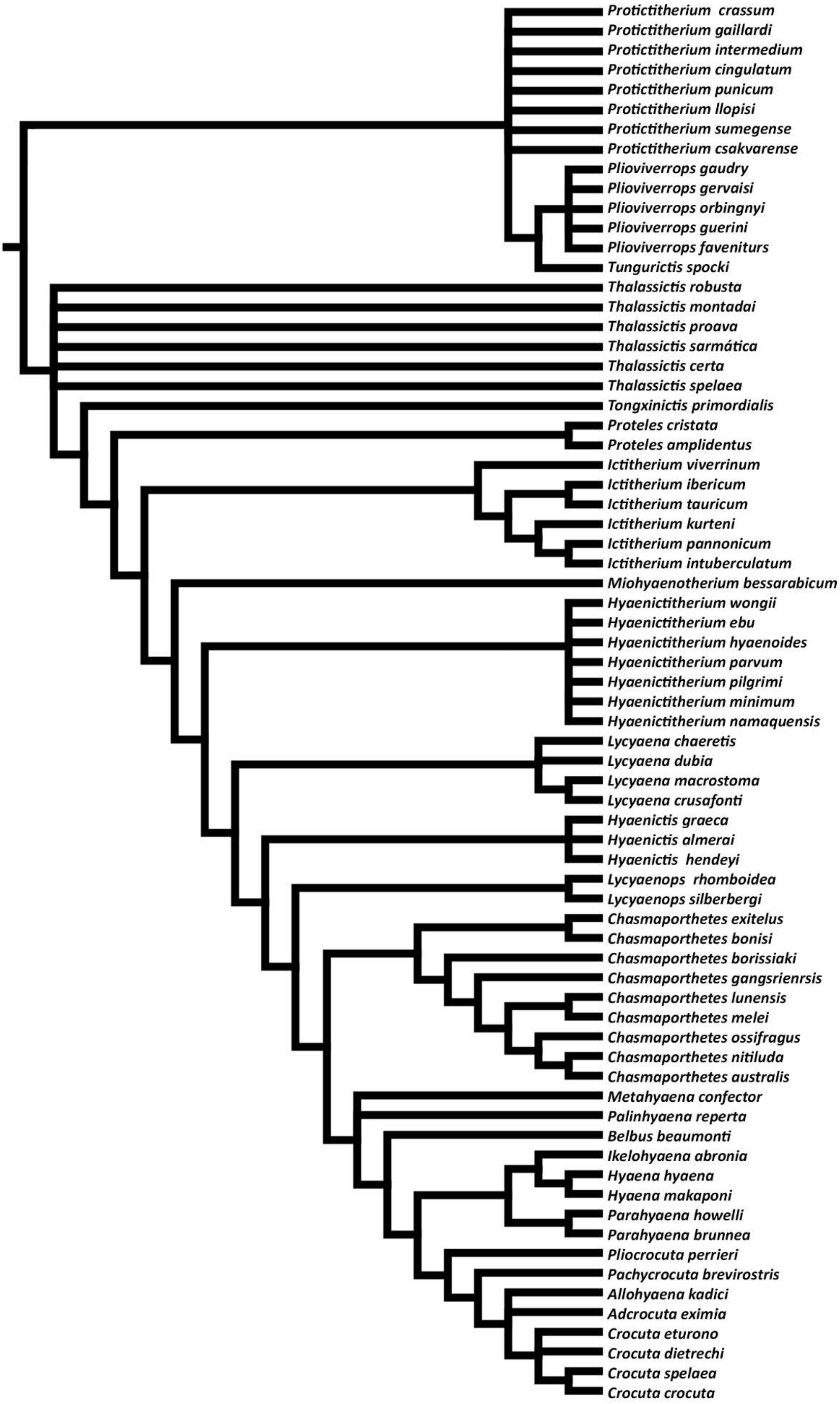

Figure 1.26: Current phylogeny of the family Hyaenidae family, including extinct species (redrawn from Turner et al., 2008).

The phylogeny of hyaenids depicted in Fig 1.26 is, with minor changes, based on the most recent version (Turner et al., 2008) of the cladistics analysis originally made by Werdelin and Solounias (1991) on the basis of 18 species and 28 cranial and postcranial characters. The remaining species within Hyaenidae have been placed accordingly to their "closest" relatives. The cladistics analysis made by Fraile (2015) has been also considered to update the relationships among the basal species.

1.2.2. Paleobiology and paleoecology

Feeding

There is a wide disparity in dental morphological traits among fossil hyaenids, which evidences the diversity of their dietary and feeding behaviors. The dentition of small and basal forms such as *Plioviverrops* and *Protictitherium* resembles that of viverrids or herpestids (Kretzoi, 1938; Schmidt-Kittler, 1976; Soria, 1980; Semenov, 1989; Fraile, 2015): full set of molars unreduced; m1 trigonid showing a larger protoconid; m1 talonid well developed with high cuspids; and narrow premolars, with a narrow but relatively high protocone and low accessory cusps (if present). The former characteristics denote an omnivorous diet, in terms of small carnivores, being these animals able to feed on small vertebrates, insects or similar food items (Schmidt-Kittler, 1976; Werdelin and Solounias, 1991, 1996).

The second set of clear characters, recognizable in the fossil record, that putatively represents a different dietary behavior is shown by medium-sized hyaenids, such as *Ictitherium* and *Hyaenictitherium* (Werdelin, 1988a, b; Semenov, 1989; Werdelin and Solounias, 1991, 1996; Werdelin and turner, 1996a; Zhang et al., 2002; Andersson and Werdelin, 2005; de Bonis, 2004,2005; Semenov, 2008; Koufos 2011): these forms reduced the m2 and m3 and enlarged the premolars; the m1 displays both protoconid and paraconid of equal height, and a reduced talonid with low cuspids; the premolars are larger and wider, with bulky accessory cusps. In general terms, this dentition is more trenchant than in the former species, but also more robust. This suggests a more carnivorous diet on the medium-size forms than in the smaller ones, and also better adaptations towards primary durophagy (Ferretti, 1999, 2007; Tseng, 2012).

Larger hyaenids, such as *Chasmaporthetes* or *Adcrocuta*, show two clear distinct morphologies in their dentition, suggesting differences in their dietary behaviors. The first group shows hypercarnivorous adaptations, whereas the second shows heavy durophagous traits. The first group would be formed by *Chasmaporthetes* and members of its clade, being characterized by the classical hypercarnivorous traits (such as the loss of the m1 talonid or the elongation of the P4 metastyle and m1 protoconid), with the exception the buccolingually more robust dentition than in felids (Kurtén, 1968; Kurtén and Werdelin 1988; Werdelin and Solounias, 1991, 1996; Werdelin et al., 1994; Rook et al., 2004; Antón et al., 2006; Tseng et al., 2013). The *Chasmaporthetes* clade has completely lost the M2 and m2, and highly reduced the M1. The carnassials are fully developed, with a long parastyle blade in the P4 and a high and trenchant trigonid in the m1, which also has a highly reduced metaconid and talonid. The premolars have high accessory cusps aligned with the protocone, forming a single line. They also have other features in the skull that resemble more hypercarnivores than durophagous carnivores, such as the straight dental row, the shallow masseteric fossa, the long muzzle, etc. (Antón et al., 2006). At last, despite their adaptations towards hypercarnivory, species of this group still have durophagous capabilities (Ferretti, 1999; Tseng et al., 2011; Tseng, 2012).

The groups of durophagous hyaenids, or bone-crackers, have the common traits already explained in previous pages (Van Valkenburgh, 1989; Kurtén and Werdelin, 1988; Werdelin and Solounias, 1991; Ferretti, 2007): enlargement of the premolars (especially P3, p3, and p4), reduction in the number of molars, curved tooth rows, and a deep masseteric fossa.

Locomotion

Nowadays, extant hyenas are cursorial, with more or less developed cursorial characters. This means, in a broad sense, that their skeletal morphology allows them to move fast in open environments. In contrast, extinct hyaenids show different degrees of cursoriality or even different types of locomotion, as evidenced by their differing postcranial adaptations. The earliest hyaenid, *Protictitherium*, shows two different ways of locomotion. Some forms appear adapted to closed environments, by possessing well-developed climbing abilities, such as the primitively retained retractile claws (Semenov, 1989; Werdelin and Solounias, 1996). Vallesian (late Miocene) speies of the genus, in contrast, display a totally different morphology (Fraile, 2015): both limbs have adaptations towards cursoriality, and the claws are not retractile, which suggests an entirely terrestrial locomotion at that time. Almost all the remaining Miocene hyaenids, from the small *Plioviverrops* to the large *Adcrocuta*, show adaptations towards terrestrial locomotion but vary in their degree of cursoriality. Medium-sized forms have a mix of adaptations, depending on the genus (Werdelin, 1988a, b; Semenov, 1989, 2008; Werdelin and Solounias, 1991, 1996; de Bonis, 2004, 2005). The most cursorial Miocene genera (and probably of the whole hyaenid fossil record) are those belonging to the

Chasmaporthetes clade, which show clear adaptations towards cursoriality in their limbs, being more adapted for running in open habitats (Kurtén, 1968; Galiano and Frailey, 1977; Berta, 1981; Kurtén and Werdelin, 1988; Werdelin and Solounias, 1991, 1996; Werdelin et al., 1994; Antón et al., 2006; Tseng et al., 2013). During the Pliocene and the Pleistocene, the bone-cracker hyenas acquired more cursorial adaptations resembling the living forms (Lewis and Werdelin, 1997; Werdelin and Lewis, 2005).

Hyaenid ecomorphotypes

As explained above, there are six different ecomorphotypes in which almost all species can be accommodated (Werdelin and Solounias, 1996; Fig. 1.27): civet-like insectivore/omnivore, mongoose-like insectivore/omnivore, jackal- and wolf-like meat and bone eaters, cursorial meat and bone eaters, transitional bone crackers, and bone crackers.

- **Type 1 (civet-like insectivore/omnivore):** This ecomorphotype displays a civet-like dentition (full set of molars and premolars; p1 characterized by a low paraconid, a high protoconid, a well-developed metaconid, and a tricuspid and large talonid). The postcranial skeleton still shows the primitive arboreal adaptations, such as the retractile claws (Semenov, 1989). These characters indicate a semiarboreal lifestyle, with a mixed diet consisting of small mammals, birds, and insects. This ecomorphotype includes all the known species of *Protictitherium* (Werdelin and Solounias, 1996). However, the recent description of several almost complete specimens of *Protictitherium crassum* from the Vallesian of Batallones (Fraile, 2015) would suggest a more terrestrial locomotor for these forms. The known chronological range of this ecomorphotype goes from MN4 to MN12 (Werdelin and Solounias, 1996; Turner et al., 2008)
- **Type 2 (mongoose-like insectivore/omnivore):** The forms of this ecomorphotype show more incipient adaptations for an insectivorous diet, with a reduced dentition and the more puncture crushing cusps on the cheek teeth. The three cuspids of the m1 trigonid are subequal in height, as a consequence of the enlarged metaconid and the reduced protoconid. The claws are not retractile, and the whole postcranial skeleton suggests a greater adaptation for terrestriality than in ecomorphotype 1. The species included in this ecomorphotype are the different forms of *Plioviverrops* and probably the Vallesian forms of *Protictitherium.* The temporal distribution of this morphotype goes from MN5 to MN14 (Torre 1989; Werdelin and Solounias, 1996; Turner et al., 2008)
- **Type 3 (jackal and wolf-like meat and bone eaters):** This ecomorphotype is one of the most widely represented in the fossil record and would be comparable to small canids, as

the hyaenids included in this ecomorphotype possess an unspecialized dentition that resembles canids such as *Vulpes*, even if with more adaptations for bone-crushing. Their dentition (when compared to ecomorphotypes 1 and 2) is characterized by a reduction of the molars, a reduction of the m1 metaconid and talonid, and the enlargement of the m1 paraconid (length) and protoconid (height). The postcranial skeleton evidences the general enlargement of the body and also displays adaptations for terrestriality without clear signs of cursoriality. The species included in this ecomorphotype belong to genera *Ictitherium*, *Thalassictis*, *Miohyaenotherium*, and *Hyaenictitherium*, being recorded from MN7+8 to MN15.

- **Type 4 (cursorial meat and bone eaters):** These forms show a trend towards the reduction of the bone-cracking abilities, or adaptations of their dentition and the enlargement of the sectorial dentition for meat eating. M2 and m2 are reduced or lost. The premolars also show progressive changes: the anterior accessory cusps are enlarged and the posterior accessory cuspid is lost in the p4. Other dental traits that show progressive changes are the loss of the p1 and the reduction/loss of the m1 metaconid. The postcranial skeleton shows clear adaptations for cursoriality, which indicates a better adaptation to open environments. These forms are recorded from MN9 to the Early Pleistocene and include the genera *Lycyaena*, *Lycyaenops*, *Hyaenictis* and *Chasmaporthetes.*
- **Type 5 (transitional bone-crackers):** This group is formed by the transitional forms to ecomorphotype 6, and includes the species *Metahyaena confector*, *Palinhyaena reperta*, *Belbus beaumonti* and *Hyaena abronia*. These forms show incipient adaptations for bone-cracking, such as the enlargement of the premolars (especially in buccolingual width) and the asymmetry of their main cusp, and the posterior accessory cuspid of the p4 is enlarged, instead of reduced as in ecomorphotype 4. The degree of cursoriality of these species is unknown due to the lack of postcranial remains. They coexist with many species of ecomorphotype 4, which given their differences would occupy a different ecological niche, more similar to the living bone-cracking hyenas. This ecomorphotype was recorded from MN9 to MN17.
- **Type 6 (bone-crackers):** These forms, which include 3 out of the 4 extant species, show highly developed adaptations for bone-cracking, basically evidenced by the extreme buccolingual enlargement of the premolars. The genera included in this ecomorphotype are *Adcrocuta*, *Allohyaena*, *Pliocrocuta*, *Pachycrocuta*, *Crocuta, Parahyaena* and *Hyaena* (except for *Hyaena abronia*). Two of them, *Crocuta* and *Pachycrocuta,* have extreme adaptations, especially in the bone-crushing complex formed by P3, p3, and p4. Additionally, *Crocuta* shows incipient adaptations for meat eating, such as the extreme

reduction of the m1 talonid, the enlargement of the m1 trigonid, and the enlargement of the P4 metastyle. Most of them display cursorial adaptations in their postcranial skeleton, like the living species, but others such as *Adcrocut*a do not (Pilgrim, 1931; Werdelin 1996). This ecomorphotype is recorded from MN10 to the present.

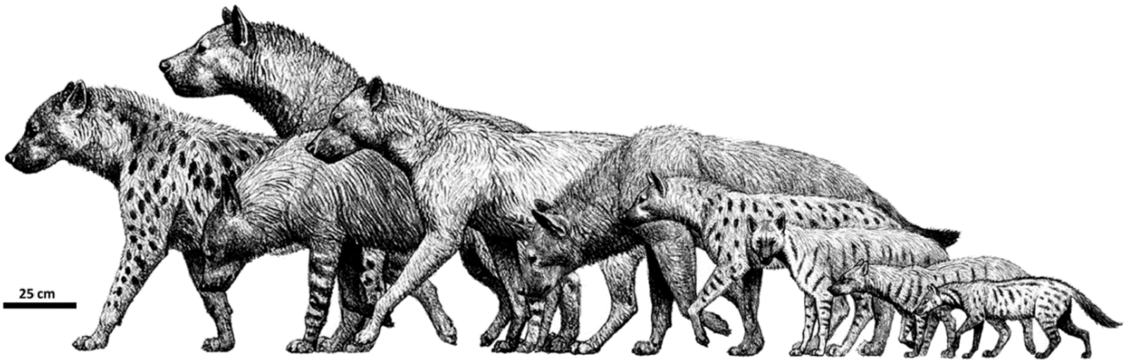

Figure 1.27: Reconstruction of selected hyaenid species representative of different ecomorphotypes. From left to right: *Plioviverrops orbignyi* (Type 2), *Protictitherium crassum* (Type 1), *Ictitherium viverrinum* (Type 3), *Hyaenictitherium wongii* (Type 3), *Adcrocuta eximia* (Type 6), *Chasmaporthetes lunensis* (Type 4), *Pliocrocuta perrieri* (Type 6), *Pachycrocuta brevirostris* (Type 6), and *Crocuta crocuta* (Type 6). Figure drawn by Mauricio Antón.

There are some species that do not fit well within any of the aforementioned ecomorphotypes: *Proteles*, due to his unique mix of myrmecophagous diet and open environment adaptations, which would make it fit between types 2, 3 or 4 (Werdelin and Solounias, 1996); *Tungurictis*, which have extreme dietary adaptations in a civet-like form, with the loss of any bone-crushing feature (Werdelin and Solounias, 1996); *Tongxinictis*, which might be closely related to the previous one, with a civet-like dentition (Werdelin and Solounias, 1996); and *Hyaenictitherium wongii*, which was originally placed within ecomorphotype 3, although the description of *Hyaenictitherium ebu* prompted to reconsider such placement, as this genus displayed more developed cursorial adaptations than those of type 3, without reaching those of type 4 (Semenov, 2008).

Social behavior

Little is known about the sociability of extinct hyaenids. Most of them have generally been considered solitary, although some species (such as those included in ecomorphotype 4 and some Plio-Pleistocene bone-crackers) have been considered gregarious (Berta, 1981; Antón et al., 2006). *Chasmaporthetes*, as previously stated, was probably the most cursorial hyena known from the fossil record, and some authors (Berta, 1981; Kurtén and Werdelin, 1988; Antón et al., 2006), on the basis of the morphology of their skull and postcranial skeleton, have considered that their ecological role should be comparable to that of *Crocuta crocuta*, which is an active hunter. Antón et al. (2006) explicitly asserted that *Chasmaporthetes* was probably gregarious (at least regarding the European *Chasmaporthetes lunensis*), based on morphological similarities with the living painted dogs: cranial shape and dental morphology adapted to provide a strong bite (like in other hyaenids and canids) and gracile limbs unable to grasp prey like felids do. These characteristics combined would have forced *Chasmaporthetes* to hunt in groups so as to be able to capture large preys. In contrast, Tseng et al. (2013) suggested the opposite, noting that gregariousness in extinct hyaenids should be inferred only on the basis of species abundance and age structure (mainly abundance of cubs, subadults and older individuals) in the studied sites. The solitary behavior inferred for *Chasmaporthetes* by Tseng et al. (2013) would be based on the recovered of scarce remains of this genus within the taphocenoses and scarce age variance (in this case, young adults).

Tseng et al. (2013) further concluded that Plio-Pleistocene bone-crackers, such as *Pliocrocuta perrieri*, *Pachycrocuta brevirostris* and *Crocuta spelaea,* were probably gregarious, based on the abundance of recovered specimens in the studied sites where they can be identified and the broad age range that these remains present in each site (from neonates to very old adult individuals). In contrast, Palmqvist et al. (2011) concluded that *Pachycrocuta brevirostris* must have been a solitary scavenger based on the bone accumulations attributed to this taxon, its limited cursorial features (with very short hindlimbs and powerful forelimbs, which putatively favored the transportation of large pieces of carrion), and the extreme durophagous adaptations of the skull. Other previous authors favored the opposite interpretation (Turner and Antón, 1996; Galobart et al., 2003; Denell et al., 2008), considering *Pachycrocuta* an active pack hunter, and therefore gregarious. The latter hypothesis is based on the same arguments as the former one but differs in its conclusions. These authors (Turner and Antón, 1996; Galobart et al., 2003; Denell et al., 2008) consider the lack of cursoriality a disadvantage when foraging, as it requires a larger amount of energy, especially for traveling long distances. On one hand, the large size is considered advantageous for subdoing large preys in groups, but in the other, it can be also disadvantageous because it requires a larger intake of food (which cannot be provided only by scavenging). Despite all these differences, most authors agree on the fact that *Crocuta spelaea* and *Pachyrcocuta brevirostris* had similar ecological roles, being either solitary or gregarious.

1.2.3. Extinct bone-cracking hyenas

The relatively reduced group of fossil bone-cracking hyenas is mainly composed of a series of monotypic genera, which are listed and detailed below in chronological order from earliest to latest forms:

***Adcrocuta*.** *Adcrocuta* is the earliest recorded hyaenid genus that shows fully developed adaptations to break bones (Fig. 1.28). This genus includes a single species, *Adcrocuta eximia*. According to Werdelin and Solounias (1991, 1996) and Turner et al. (2008), this species is characterized by well-developed and conical premolars with reduced or absent accessory cusps, a reduced P4 protocone, the presence of P1, and a broad and short palate.

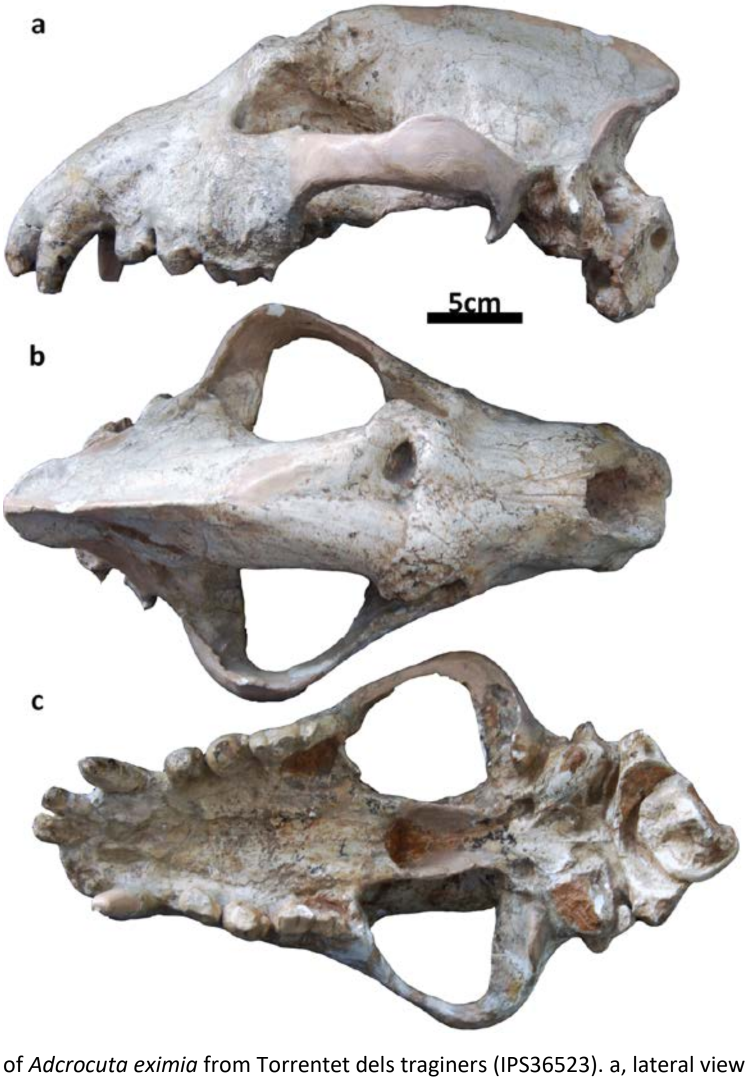

Figure 1.28: Skull of *Adcrocuta eximia* from Torrentet dels traginers (IPS36523). a, lateral view; b, dorsal view; c, occlusal view. Photos taken by Victor Vinuesa.

The postcranial remains of *Adcrocuta* from Pikermi suggest that it was a robust and a powerful animal, even if not very fast-moving, not displaying the cursorial adaptations present in the extant bone-cracking hyenas. Werdelin and Solounias (1990, 1991) and Howell and Petter (1985) considered *Adcrocuta* the sister taxon of *Crocuta crocuta*, but such an opinion has always been controversial (Werdelin and Solounias, 1991), and some authors have a different opinion, including *Adcrocuta* as a sister taxon of all other modern hyaenines (Wagner, 1998). This genus is recorded in the late Miocene from MN10 to MN13 (ca. 9.7–4.9 Ma; Turner et al., 2008) from several European localities (Werdelin and Solounias, 1991; Turner et al. 2008): Kalimantsi and Hadgimidovo in Bulgaria; Mont Luberon in France; Dytiko, Halmyropotamos, Pikermi, Prokoma, Ravin de la Pluie, and Ravin des Zouaves 1 and 5 in Greece; Dorn Durkheim in Germany; Kohfidisch in Austria; Arquillo de la Fontana, Concud, Los Mansuetos, Masía del Barbo and Torrentet dels Traginers/Piera in Spain; and Upper and Middle Maragheh in Iran, among others.

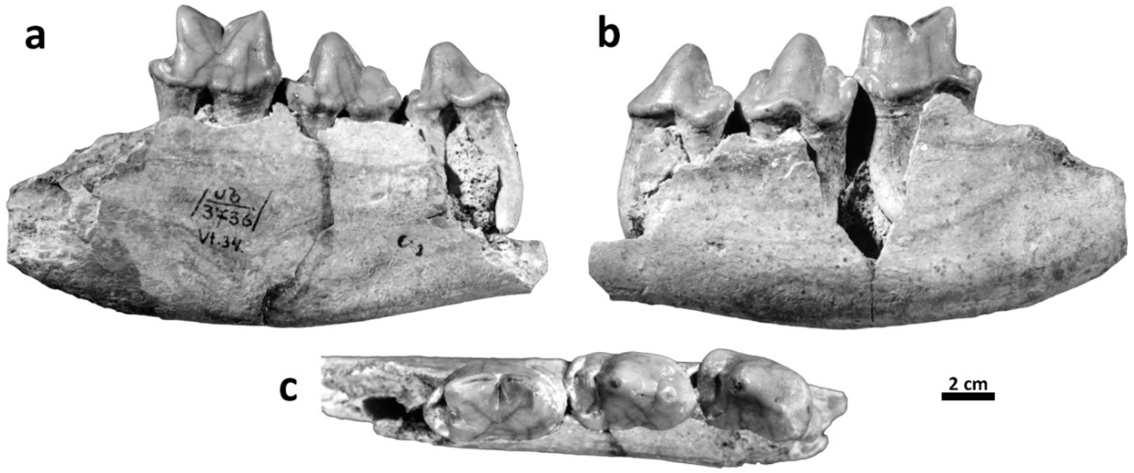

Figure 1.29: Mandibular remains from the holotype of *Allohyaena kadici*: a, lingual view; b, buccal view; c, occlusal view. Photos taken by Lars Werdelin.

***Allohyaena*.** A single species is included in this genus, *Allohyaena kadici*. Formerly included in the family Percrocutidae (Howell and Petter, 1985), it was recently relocated within the Hyaenidae (Werdelin and Kurtén, 1999). According to the latter authors, *Allohyaena kadici* (Fig. 1.29) has a mixture of primitive characters (dp4 morphology similar to that of *Hyaenictitherium*, retention of m2, long and slender premolars and large protocone on P4) and derived characters (preparastyle on P4, internal root on P3, and a uniquely derived talonid structure on the m1). These authors considered this taxon as a bone-cracker hyena, similarly to *Pachycrocuta* and *Adcrocuta*, and related it to the latter on phylogenetic grounds. Turner et al. (2008) considered this genus as the sister taxon of *Adcrocuta* and *Crocuta* (see section 1.2.1

"Systematics and phylogeny" above). This genus is scarcely recorded, known only from three localities in Europe, dated to MN 11 (ca. 8.7–9.5 Ma, late Miocene; Turner et al., 2008): Esterházy Cave and Csávkár in Hungary; and Dorn-Dürkheim in Germany.

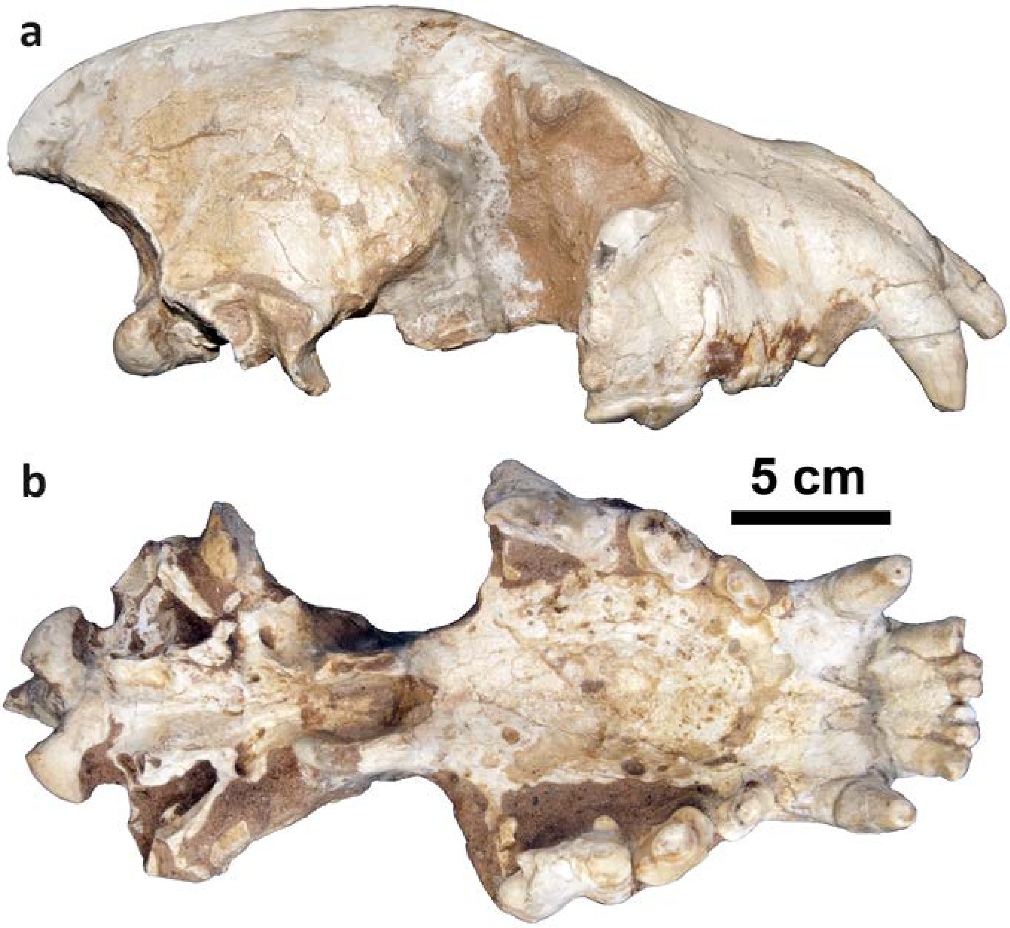

Figure 1.30: Cranial and mandibular remains of *Pliocrocuta Perrieri* (IPS36759) from Villarroya: a) lateral view; b) occlusal view. Photos by Victor Vinuesa.

***Pliocrocuta*.** This monotypic genus (Fig. 1.30), which currently includes *Pliocrocuta perrieri* as its type and only species, is the commonest Eurasian Late Pliocene-Early Pleistocene (Early to Middle Villafranchian) bone-cracking hyaenid. Werdelin and Solounias (1991) and Turner (1990) removed this species from *Pachycrocuta,* where it had been included by Howell and Petter (1980), and reallocated it into *Pliocrocuta*, further considering it as a senior subjective synonym of other species previously considered valid, such as *Pliocrocuta pyrenaica* Depéret, 1890. It is recorded from MN13 to the Early Pleistocene (ca. 5–2 Ma; Tseng et al., 2015). In the past, this species was suggested to be distributed in two different time intervals, with an apparent extinction around 2 Ma (Turner et al., 2008), followed by its purported reappearance during the Middle Pleistocene in central Europe and some southern French and Portuguese sites (Turner et al., 2008). Currently, however, it is considered that its former extinction was real and that its supposed reappearance corresponds in fact to an early Middle Pleistocene dispersal event of the genus *Hyaena* from Africa (Madurell-Malapeira, 2010). This genus is considered the sister taxon of *Pachycrocuta* (Turner et al., 2008), being deemed by many authors as its direct ancestor (see section 1.2.1 “Systematics and phylogeny” above; Olive, 2006; Turner et al., 2008). It is characterized by thick premolars with reduced accessory cusps, resembling the morphology of the extant *Crocuta*, with reduced m1 metaconid and talonid (Olive, 2006). *Pliocrocuta perrieri* has been recorded from multiple European localities (Turner et al., 2008): Hollabrum in Austria; Ardé, Etouaires, Es-Taliens, Chiliac, Pardines, Perpignan, Sénèze, Serrat-d´En-Vacquer, St. Vallier and Vialette in France; Erpfinger Höhle, Greusnach, Gundersheim 1 and 4 in Germany; Hajnácka in Slovakia; Red Crag deposits in England; Gerakarou, Sesklon and Petralona in Greece; Montopoli and Tasso in Italy; Tegelen in the Netherlands; and La Calera II, El Rincón, La Gloria 4, La Puebla de Valverde, Layna and Villarroya in Spain.

Pachycrocuta. *Pachycrocuta brevirostris* (Gervais, 1850) is the only species included in this genus. This hyena is considered the largest hyena that ever existed, weighing roughly from 90 to 150 kg, and fits perfectly within the ecomorphotype of fully developed bone-crackers due to its craniodental features (Fig. 1.31), which include broad premolars (especially P3 and p4) with reduced accessory cusps as well as reduced m1 talonid and metaconid. Their distinctive characters are very similar to those of *Pliocrocuta*, except for the larger size, skeletal stoutness and the more developed dental characters, following the evolutionary trend already displayed, albeit to a lesser extent, by *Pliocrocuta* in the reduction of accessory premolar cusps and the reduction of m1 metaconid and talonid (Olive, 2006). This species is recorded in the Old World from MN15 to the Epi-Villafranchian (ca. 4.1–0.83 Ma; Turner et al., 2008; Turner and Antón, 1996, Madurell-Malapeira et al., 2010; Werdelin and Peigné, 2010). In Europe, it has been documented from 1.8 to 0.86 Ma in the following localities (Werdelin and Solounias, 1991; Turner et al., 2008; Madurell-Malapeira, 2010): Stránskà Skàla in the Czech Republic; Bacton, Mundesley, Sidestrand and Westbury-sub-Mendip in England; Sainzelles, Ceyssaguet and Vallonnet in France: Süssenborn, Untermassfeld and Würzburg-Schalksberg in Germany; Gerakarou, Apollonia and Petralona in Greece; Gombaszoeg in Hungary; Olivola, Casa Frata and Pirro Nord in Italy; Cueva Victoria, Venta Micena, Almenara 1, Pontón de la Oliva, Barranco León 5, Fuenta Nueva 3, Cueva Victoria, Incarcal and in the Vallparadís Section in Spain, among others.

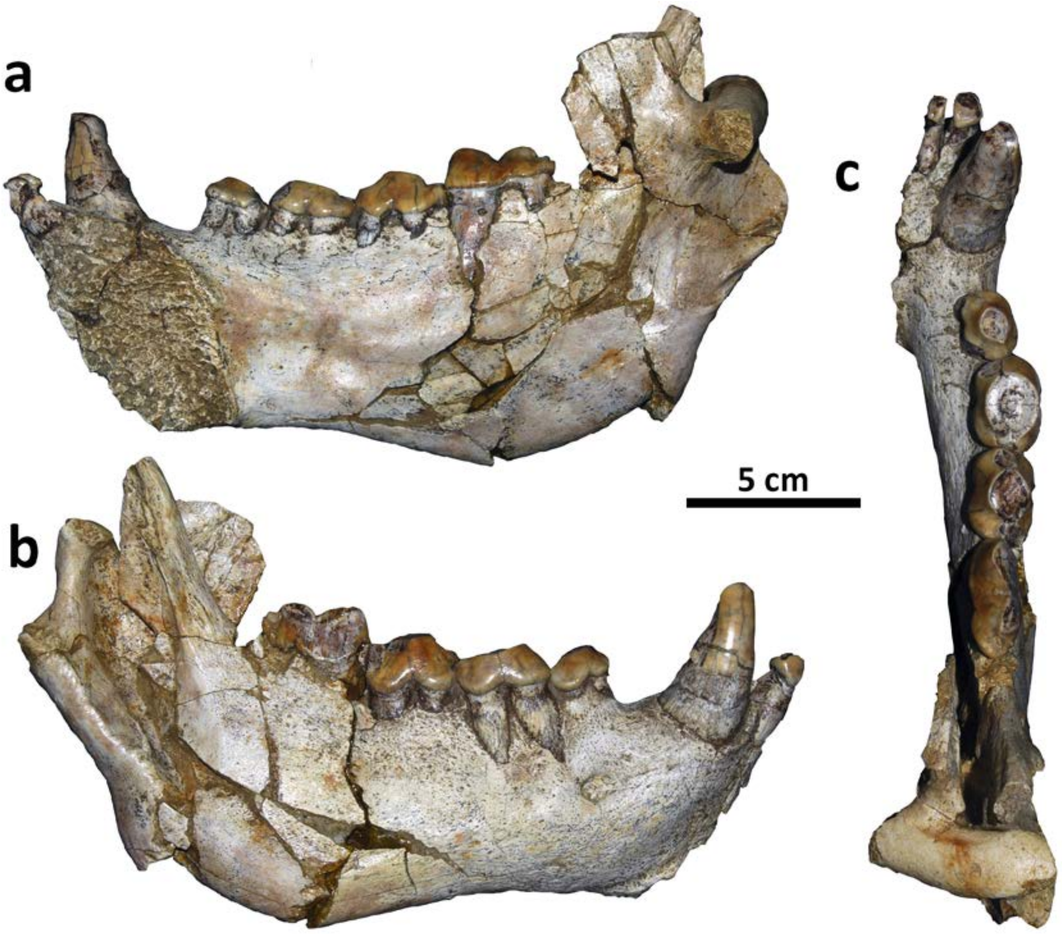

Figure 1.31: Mandibular remains (EVT24641) of *Pachycrocuta brevirostris* from the Vallparadis section in Terrassa: a, lingual view; b, labial view; c, occlusal view. Photos taken by Joan Madurell-Malapeira.

1.2.4. Evolutionary history

The evolutionary history of hyaenids is long and complex and has been the topic of several works focused on the evolutionary changes across Europe or Asia (Werdelin and Solounias, 1991, 1996; Werdelin, 1996; Tseng and Wang, 2007; Turner et al., 2008; Tseng et al., 2013), although some recent works also focused on Africa (Werdelin and Turner, 1996b; Werdelin and Peigné, 2010). The scarce presence of this group in North America is not widely studied, although some works focus a bit on it (Kurtén and Werdelin, 1988; Werdelin and Solounias, 1991).

Origin and diversification of hyaenids

The origin of hyaenids and their divergence from other feliforms according to the fossil record and molecular data is dated back at least to 25 Ma (Koepfli et al., 2006; section 1.1.2), although their divergence might have taken place slightly earlier (Werdelin and Solounias, 1991). The hypothetical last common ancestor of hyaenids would be related to either herpestids or viverrids, but the geographical area of origin is unknown. The problem with the early stages of hyaenid evolution is the difficulty to clearly distinguish between basal hyaenids, basal herpestids, such as *Herpestides antiquus* de Blainville, 1842 and basal viverrids (such as *Progenetta* Depéret, 1892), as they share several craniodental features, such as the m1 and M1 morphology, or the tympanic bulla development (Werdelin and Solounias, 1991). The earliest species clearly included within the family appears for the first time in Western Europe (Fig. 1.32; Werdelin and Solounias, 1991, 1996; Turner et al., 2008), i.e., *Protictitherium gaillardi* (MN4, Bézian; Ginsburg and Bulot, 1982; Werdelin and Solounias, 1996), followed by *Plioviverrops gervaisi* (MN5, Vieux Collognes; Mein, 1958, 1979; Savage and Russell, 1983; Mein, 1989). These early hyaenids belong to ecomorphotypes 1 and 2, and were, therefore, generalists, eating small mammals, birds or insects, and having both arboreal and terrestrial locomotion (Werdelin and Solounias, 1996). Slightly later, during the MN5–MN6 a small faunal turnover was documented in western Europe (Werdelin and Solounias, 1996), probably linked to the Parathetys Badenian salinity crisis (Rögl and Steininger, 1983) and more species of ecomorphotypes 1 and 2 appeared (Fig. 1.32), and the first occurrence of the family in central Europe and Asia is documented (Werdelin and Solounias, 1996), including the appearance of *Tongxinictis* in China (Qiu et al., 1988a; Qiu, 1989). During MN7+8, ecomorphotype 3 made its first appearance with the earliest records of *Thalassictis* in Western Europe (Werdelin and Solounias, 1996). This ecomorphotype 3, characterized by highly reduced molars, probably evolved from members of the terrestrial ecomorphotype 2 (Werdelin and Solounias, 1996).

At the beginning of the MN9 (Werdelin and Solounias, 1996) and during the Vallesian, hyaenids increased in diversity, with the appearance of several species included in all the different ecomorphotypes (Werdelin and Solounias, 1991, 1996; Turner et al., 2008). Ecomorphotype 3 substantially increased diversity with the record of genera *Ictitherium* and *Hyaenictitherium* in Eurasia, being the first only present in Europe (Werdelin and Solounias, 1996; Tseng and Wang, 2007). *Ictitherium*, although included within ecomorphotype 3, displays less reduced molars, as well as less cursorial adaptations, which suggests that it originated from some member of ecomorphotype 2, instead of the previously known species from ecomorphotype 3, thereby suggesting a polyphyletic origin for the Ictitheriinae (Werdelin and Solounias, 1996). *Hyaenictitherium*, which ended up being highly successful (considering its long temporal range and wide spatial distribution across Eurasia), displays reduced posterior molars, like *Thalassictis*, as well as a less sectorial dentition, like *Ictitherium* (Semenov, 1989; Werdelin and Solounias, 1996). Western Eurasia is also the first region where both ecomorphotypes 5 and 6 first appeared during the Vallesian, with the respective earliest records of *Metahyaena* in Turkey (Viranta and Werdelin, 2003; Turner et al., 2008) and *Adcrocuta* in Spain and France (Soria, 1980; de Bonis and Koufos, 1981; Howell and Petter, 1985; Werdelin and Solounias, 1990, 1991). The genera *Metahyaena* and *Adcrocuta* were probably able to coexist with all hyaenids from other ecomorphotypes due to their different ecological niche, their diet being more adapted for scavenging (Werdelin and Turner, 1996a; Werdelin and Solounias, 1996). The evolution of ecomorphotypes 5 and 6 at this time must have occurred from species of ecomophotype 3 in eastern Europe, probably from *Hyaenictitherium* (Howell and Petter, 1985; Werdelin and Solounias, 1990), although the fossil record places it in Western Eurasia. In parallel to this, there was a major faunal renewal between southern Europe and northern Africa (Thomas et al., 1982; Bernor, 1983, 1984), and as a consequence hyaenids are first recorded in Morocco (Beni Mellal) and Tunisia (Bled Douarah; Werdelin and Solounias, 1991, 1996; Werdelin and Turner, 1996b; Werdelin and Peigné, 2010), being represented by species of ecomorphotype 1 (*Protictitherium punicum* and *Protictitherium crassum*) as well as the first record of *Lycyaena crusafonti*, from ecomorphotype 4. The origin of this later ecomorphotype in Africa is uncertain (Werdelin and solounias, 1996), especially considering the appearance of *Hyaenictis almerai* in the Iberian Peninsula at the MN10 (Villalta Comella and Crusafont Pairó, 1948; Turner et al., 2008). Finally, larger forms of *Hyaenictitherium* started to appear in Asia approximately by this time (Werdelin and Solounias, 1996).

During the Turolian (MN11-MN13), hyaenids reached their maximum peak of diversity, both in terms of species and ecomorphotype numbers (Werdelin and Solounias, 1991, 1996; Turner et al., 2008). The larger forms of the hypercarnivorous ecomorphotype 4, included within *Chasmaporthetes*, appear by this time, although it is unknown if they evolved from ecomorphotype 3 species already present in Eurasia, or from pre-existing species of ecomorphotype 4, such as *Lycyaena crusafonti*, which could have come back from northern Africa (Werdelin and Turner, 1996b). These early members of ecomorphotype 4 include the oldest species of *Chasmaporthetes,* but also most of the *Hyaenictis* and *Lycyaena* species. Furthermore, during the Turolian, new species from ecomorphotypes 5 and 6 appear in Asia, Europe, and Africa. Three species included within ecomorphotype 5 appear in the Old World (Werdelin and Solounias, 1991; Werdelin and Turner, 1996b; Werdelin and Lewis, 2005; Werdelin and Sander, 2010): *Palinhyaena* in Asia, *Belbus* in Europe, and *Ikelohyaena* in Africa. The huge bone-cracker *Adcrocuta* is recorded outside of Europe during the Turolian, more precisely in China and North Africa; and a new genus, *Allohyaena*, appears in central Europe (Howell and Petter, 1985; Werdelin and Solounias, 1990; Werdelin and Kurtén, 1999; Turner et al., 2008).

After the Miocene-Pliocene boundary, a marked decrease in the number of hyaenid species was recorded in the Old World. The later fact was a consequence of the faunal renewal recorded across such transition, since only 32 of 59 Carnivore species recoded during the Turolian were recorded in the early Pliocene (Savage and Russell, 1983; Werdelin and Solounias; 1996; Werdelin and Turner, 1996a, b; Turner and Antón, 2004). Nevertheless, the decreasing in hyaenid diversity started earlier, during the middle Turolian, with the disappearance of almost all members of ecomorphotypes 1 and 2, as well as, the progressive decrease in the number of species ascribed to the ecomorphotypes 3 and 4 (Werdelin and Solounias, 1991, 1996; Werdelin and turner, 1996a, b; Turner at al., 2008). The later fact could be related with the first arrival of canids into the Old World during the second half of the Turolian, since these taxa replaced hyaenids in most of their niches (Werdelin and Turner, 1996a, b; Turner and Antón, 2004). Thus, at the beginning of the Pliocene (Ruscinian, MN14), the ecomorphological diversity of hyaenids in Eurasia is reduced to ecomorphotypes 4 and 6, respectively with the genera *Chasmaporthetes* and *Pliocrocuta* as the only representatives of the family (Howell and Petter, 1980; Werdelin and Solounias, 1991, 1996; Turner et al., 2008). In contrast, during the Pliocene, hyaenids dispersed into America for the first time (Kurtén and Werdelin, 1988; Werdelin and Solounias, 1991, 1996; Werdelin et al., 1994). The genus that settled in the new world, *Chasmaporthetes*, belongs to ecomorphotype 4 (the cursorial meat-

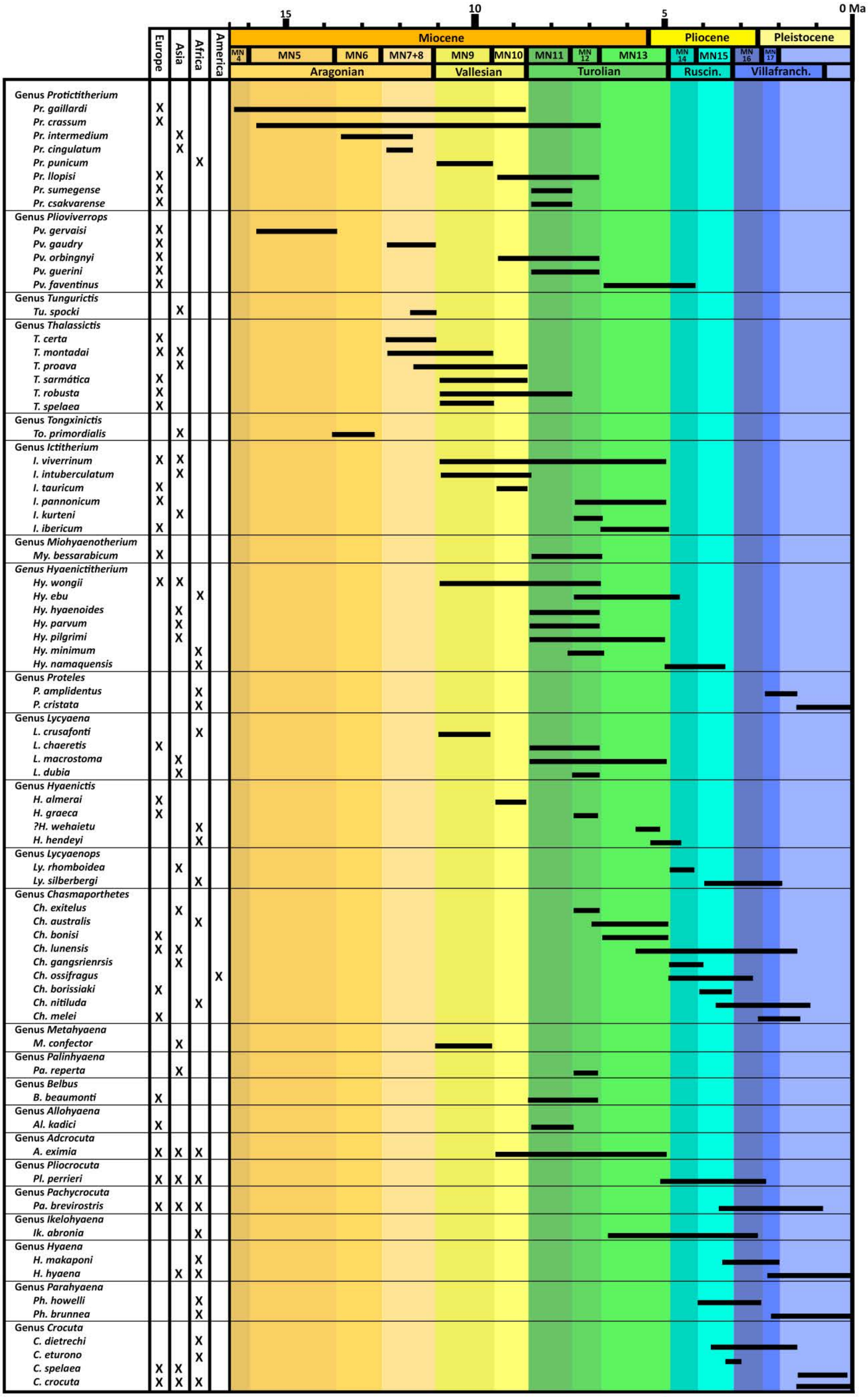
15
10
5
0 Ma
Europe
Asia
Africa
America
Miocene
Pliocene
Pleistocene
MN4
MN5
MN6
MN7+8
MN9
MN10
MN11
MN12
MN13
MN14
MN15
MN16
MN17
Aragonian
Vallesian
Turolian
Ruscin.
Villafranch.
Genus Protictitherium
Pr. gaillardi
Pr. crassum
Pr. intermedium
Pr. cingulatum
Pr. punicum
Pr. llopisi
Pr. sumegense
Pr. csakvarense
Genus Plioviverrops
Pv. gervaisi
Pv. gaudry
Pv. orbingnyi
Pv. guerini
Pv. faventinus
Genus Tungurictis
Tu. spocki
Genus Thalassictis
T. certa
T. montadai
T. proava
T. sarmática
T. robusta
T. spelaea
Genus Tongxinictis
To. primordialis
Genus Ictitherium
I. viverrinum
I. intuberculatum
I. tauricum
I. pannonicum
I. kurteni
I. ibericum
Genus Miohyaenotherium
My. bessarabicum
Genus Hyaenictitherium
Hy. wongii
Hy. ebu
Hy. hyaenoides
Hy. parvum
Hy. pilgrimi
Hy. minimum
Hy. namaquensis
Genus Proteles
P. amplidentus
P. cristata
Genus Lycyaena
L. crusafonti
L. chaeretis
L. macrostoma
L. dubia
Genus Hyaenictis
H. almerai
H. graeca
?H. wehaietu
H. hendeyi
Genus Lycyaenops
Ly. rhomboidea
Ly. silberbergi
Genus Chasmaporthetes
Ch. exitelus
Ch. australis
Ch. bonisi
Ch. lunensis
Ch. gangsrienrsis
Ch. ossifragus
Ch. borissiaki
Ch. nitiluda
Ch. melei
Genus Metahyaena
M. confector
Genus Palinhyaena
Pa. reperta
Genus Belbus
B. beaumonti
Genus Allohyaena
Al. kadici
Genus Adcrocuta
A. eximia
Genus Pliocrocuta
Pl. perrieri
Genus Pachycrocuta
Pa. brevirostris
Genus Ikelohyaena
Ik. abronia
Genus Hyaena
H. makaponi
H. hyaena
Genus Parahyaena
Ph. howelli
Ph. brunnea
Genus Crocuta
C. dietrechi
C. eturono
C. spelaea
C. crocuta
X

Figure1.32 (previous page): Chronological chart that details the chronostratigraphic range (in Ma) and MN biozonation for all the known hyaenid species, as well as their geographical distribution by continents.

eaters), as the bone-cracker niche was already occupied by borophagine canids (Munthe, 1989; Werdelin, 1989). In contrast, Africa offered shelter for some hyaenids that went extinct in Eurasia with the arrival of canids, which explains why species from the genera *Hyaenictitherium*, *Hyaenictis*, and *Lycyaenops* survived a bit longer beyond the Mio-Pliocene boundary, and others like *Ikelohyaena*, *Chasmaporthetes* and the ancestor of *Proteles* survived there far beyond it (Werdelin et al., 1994; Werdelin 1996; Werdelin and Turner, 1996b; Werdelin and Peigné, 2010). According to the fossil record, the evolution of the extant genera took place after the Miocene-Pliocene boundary in Asia or Africa, from primitive forms of ecomorphotypes 3 or 4, and subsequently ecomorphotype 5, probably from the genus *Hyaenictitherium* in the case of the bone-crackers (Howell and Petter, 1980; Werdelin and Turner, 1996b; Werdelin and Peigné, 2010).

In Europe, several changes in faunal dynamics during the Pleistocene affected the already low diversity of hyaenids. At the middle-late Villafranchian boundary (ca. 1.8 Ma), *Pliocrocuta* was replaced by the giant *Pachycrocuta*, whereas *Chasmaporthetes* becames extinct, reducing the number of ecomorphotypes to a single one (the bone-crackers; Howell and Petter 1980; Werdelin and Solounias, 1991, 1996; Turner et al., 2008). Finally, during the Villafranchian-Galerian faunal renewal (from 1.2 to 0.8 Ma), *Pachycrocuta* disappeared from Western Europe, being replaced by the smaller *Crocuta crocuta* from Africa (Turner, 1995; García and Arsuaga, 1999; Antón et al., 2005). Also, across Asia, Africa and North America, the last members of ecomorphotype 4, mostly *Chasmaporthetes*, went extinct during the Early Pleistocene (between ca. 2 and 1 Ma), resulting in the current reduced ecomorphological diversity of hyaenids, with only ecomorphotype 6 and the insectivorous *Proteles* (Werdelin and Solounias, 1991, 1996; Qiu, 1987; Werdelin and Turner, 1996b; Werdelin and Peigné, 2010).

The evolution of bone-cracking hyenas

The bone-cracking ecomorphotype appeared during the late Miocene, when transitional bone-cracking hyenas are recorded during the MN9 in Turkey (Viranta and Werdelin, 2003). Although it is unknown if all the bone-cracking genera are monophyletic or evolved convergently, it is likely that all bone-cracking hyenas emerged from a species of the genus *Hyaenictitherium* (Howell and Petter, 1985; Werdelin and Solounias, 1990). One of the major differences that distinguish the early stages of this group from ecomorphotype 4 is related to the enhanced durophagous adaptations of the latter as reflected on their p4 morphology, since bone-crackers tend to retain the p4 distolingual cingulum without enlarging the distal accessory cuspid, whereas members of ecomorphotype 4 tend to eliminate the distolingual cingulum and expand the distal accessory cuspid in a more hypercarnivorous way (Werdelin et al., 1994). The first fully developed bone-cracker, *Adcrocuta*, appears in Europe at ca. 9 Ma (Howell and Petter, 1985; Werdelin and Solounias, 1991). Its hypothetical ancestor is unclear, probably having evolved from a more primitive hyena of ecomorphotype 3 such as *Hyaenictitherium*, due to the lack of cursorial adaptations (Werdelin and Solounias, 1990, 1991, 1996). It is also unclear if the origin of this ecomorphotype took place in Asia (Schmidt-Kittler, 1976) or in Europe (Howell and Petter, 1985), although their earliest records come from Western Europe during the Vallesian (Soria, 1980; de Bonis and Koufos, 1981; Howell and Petter, 1985) and they are not documented in Asia and Africa until the middle and late Turolian, respectively (Howell and Petter, 1985; Werdelin and Lewis, 2005; Werdelin and Peigné, 2010). *Adcrocuta* possesses a mix of both durophagous and hypercarnivorous adaptations, including the enlargement of the premolars, as well as the elongation of P3 and m1, and the reduction of the P4 protocone (Werdelin and Solounias, 1991, 1996; Turner and Antón, 1996a; Turner et al., 2008), although it has generally been considered a scavenger (Werdelin and Solounias, 1991; Werdelin and Turner, 1996a, b; Turner et al., 2008). On the other hand, *Allohyaena* (the other Turolian bone-cracker) is scarcely known, being only referred in the literature as a large hyena with durophagous adaptations in the cheek teeth (Werdelin and Kurtén, 1999; Turner et al., 2008).

Pliocrocuta, the most common Pliocene and Early Pleistocene bone-cracking hyena, is recorded for the first time in China in the Early Pliocene (ca. 5–5.6 Ma; Qiu, 1987; Werdelin and Solounias, 1991; Tseng et al., 2015), and slightly later in Europe and Africa (ca. 4.2 Ma and 3.4 Ma, repectively; Werdelin and Solounias, 1991; Werdelin and Lewis, 2005; Turner et al., 2008; Werdelin and Peigné, 2010), suggesting a fast extension across the Old World, alongside the most derived members of the genus *Chasmaporthetes*, which also seem to have evolved in Asia (Tseng et al., 2013, 2015). In contrast, the giant short-faced hyena *Pachycrocuta* is first recorded in Africa in the Early Pliocene (ca. 4 Ma; Howell and Petter, 1985; Werdelin and Solounias, 1991; Werdelin, 1999; Turner and Antón, 1996; Turner et al., 2008), although its dispersal into Eurasia did not take place until much later, not being recorded until 2.6 Ma in Asia and ca. 1.8 Ma in Europe, replacing gradually *Pliocrocuta* (Howell and Petter; 1985; Qiu, 1987; Werdelin and Solounias, 1991; Turner and Antón, 1996; Turner et al., 2008). The craniodental evolutionary trend towards durophagy in the *Pliocrocuta-Pachycrocuta* lineage, as well as the noteworthy enlargement of P3, and the co-existence with *Chasmaporthetes,* suggest scavenging behavior (Howell and Petter, 1985; Turner and Antón, 1996; Palmqvist et al., 2011).

In turn, the origin of the lineage that includes the living *Hyaena* and *Parahyaena* remains unclear, although the first genus consiered to belong to this clade, *Ikelohyaena*, appears quite early (6.5 Ma) in eastern and southern Africa, suggesting that continent as the origin of this lineage (Werdelin and Solounias, 1991; Werdelin and Turner, 1996b; Werdelin and Lewis, 2005; Werdelin and Peigné, 2010). This genus retains primitive characters, such as the presence of m2, and it is not clear whether it precedes the split between *Hyaena* and *Parahyaena* (Werdelin and Lewis, 2005; Werdelin and Peigné, 2010). After the appearance of the genus *Ikelohyaena,* the evolutionary history of *Hyaena* is quite linear (with the exception of the *Parahyaena* divergence). *Hyaena hyaena* is considered to derive from *Hyaena makaponi*, with the two species slightly overlapping in time (*H. makaponi*: 3.6–2 Ma; *H. hyaena*: 2.5 Ma-present; Werdelin and Peigné, 2010). At some unknown point during the Pleistocene, *Hyaena* dispersed into Asia, where it is still extant. The lineage of *Parahyaena* and its evolution after the divergence from the *Hyaena* lineage is quite similar but restricted to Africa. The earliest species is *Parahyaena howelli*, recorded in the locality of Kanapoi (Kenya) at 4.1 Ma (Werdelin, 2003), thereby suggesting an origin in eastern Africa, instead of southern part of Africa, where it is restricted nowadays (Werdelin and Barthelme, 1997; Werdelin and Peigné, 2010).

In contrast, the origin and evolutionary history of the spotted hyena are complex and under ongoing debate. Although the earliest records of the genus are located in Africa, with two different species, *Crocuta dietrechi* and *Crocuta eturono*, recorded at ca. 4–3 Ma, the origin of the genus is controversial (Turner, 1990; Lewis and Werdelin, 1997, 2000; Werdelin and Lewis, 2005, 2008). The most likely scenario implies a succession of different species that evolved from an early, small and primitive ancestor, *Crocuta dietrechi*, with subsequent species geographically and/or temporally separated from each other, showing adaptations to local conditions. According to such a scenario, the *Crocuta* lineage might have evolved from smaller to larger forms, including the genera putatively ancestral to the genus, *Palinhyaena* or *Belbus* (Werdelin and Solounias, 1991). The later dispersals of *Crocuta* into Eurasia and the emergence of the living species *C. crocuta* are also controversial (Lewis and Werdelin, 1997; Rohland et al., 2005; Sheng et al., 2014). Recent works hypothesized two major dispersal events from Africa into Eurasia, at ca. 2.5 and 0.8 Ma, as well as their posterior extinction in Eurasia ca. 20 ka, with progressively more derived characters toward a more hypercarnivorous diet (such as the larger body size, changes in the forelimbs and the elongation of the P4 and m1) being recorded in *Crocuta spelaea* (Lewis and Werdelin, 1997, 2000; García and Arsuaga

2001; Qiu et al., 2004; Sardella and Petrucci 2012). Additionally, recent DNA studies have also confirmed the existence of gene flow between the African and Eurasian populations of spotted hyenas throughout the Pleistocene, suggesting three successive dispersal events instead of two (Rohland et al., 2005). On the basis of these molecular data, these events would have taken place at <3.5 Ma (Eastern Asia), 1.5–1.3 Ma (Europe and South Africa) and <130 ka (Eurasia). However, this does not resolve the origin of the extant *C. crocuta*. In contrast, Sheng et al. (2014) suggested two successive migrations from Eurasia into Africa at 430 ka and 63 ka, as well as a Eurasian origin for the extant *C. crocuta*. The bone-accumulating abilities of *Crocuta* across Pleistocene sites from the Old World suggest that until very recently this genus relied more on scavenging than in active hunting (e.g., Turner and Antón 1996; Boaz et al., 2000; Palmqvist et al., 2011).

Chapter 2. Geological background

The fossil remains studied in this dissertation come from different sites, mainly located in the Iberian Peninsula. The following pages provide a general description of eight sites divided into two big blocks: those from the Vallès-Penedès Basin and those from elsewhere in Eurasia.

2.1. Vallès-Penedès

Geographically, the Vallès-Penedès Basin is an elongated basin of NE-SW direction that is located in the northeastern Iberian Peninsula. Geologically, the basin is a half-graben situated between the Littoral and Prelittoral mountain ranges, which originated due to the Neogene rifting that took place in the NW Mediterranean region (Fig. 2.1; Cabrera and Calvet, 1990; Bartrina et al., 1992; Roca and Guimerà, 1992; Cabrera et al., 2004).

The half graben is limited in the NW by the Vallès-Penedès fault, with an approximate leap of 3000 m and an orientation that oscillates between ENE-WSW to NE-SW. The southern limit is delimited by a series of faults with low leap that separate it from the nearest horst (Bartrina et al., 1992). These operated as directional faults during the compressive phase of the Alpine Orogeny (Eocene-early Oligocene), but during the late Oligocene unti the middle Miocene, they operated as normal faults, originating the present system of horsts and grabens (Roca et al., 1999). The tectonic subsidence in this particular case took place differentially in each margin of the basin, originating the thickest accumulations (fault separation of over 3000 m) towards the north of it (Cabrera, 1991; de Gibert and Casanovas-Vilar, 2011).

Most of the sediments of the basin are Miocene in age, with a predominant continental origin, although there are also marine and transition sediments on the SE part of the basin. The Miocene deposits of the Vallès Penedès Basin are grouped in four large sedimentary units (Cabrera, 1981; Cabrera and Calvet, 1996; Agustí et al., 1985; de Gibert and Casanovas-Vilar, 2011)

Basal Breccia Unit: This small unit constitutes the base of the Miocene sedimentation in the basin, and chronologically corresponds to the early Miocene (Ramblian; Casanovas-Vilar et al., 2010; de Gibert and Casanovas-Vilar, 2011). It is formed by breccia deposits and conglomerates mainly of colluvial origin, with a detritic origin from the pre-Miocene sediments placed stratigraphically below (de Gibert and Casanovas-Vilar, 2011)

Lower Continental Complexes: These sediments were deposited during the early Miocene (Ramblian-early Aragonian; MN3-MN4); two subunits can be distinguished. The lower subunit, which is the most extensive, being formed by red conglomerates and breccias, attributed to small alluvial fans coming from the Littoral Range (Cabrera, 1981; Cabrera et al., 2004; de Gibert and Casanovas-Vilar, 2011; Casanovas-vilar et al., 2016a, b). The upper subunit is formed by lutites and carbonates, with sporadic evaporitic layers, that have been attributed to small lacustrine systems developed in the SE margin of the basin (Cabrera, 1981; Gibert and Casanovas, 2011; Casanovas-Vilar et al., 2011, 2015, 2016 a, b).

Marine and Transitional Complexes: This unit is manly formed by marine sediments deposited throughout a series of marine transgressions, coming from the Mediterranean connection at the S, that took place during the Middle Miocene (de Gibert and Casanovas-Vilar, 2011; Casanovas-Vilar et al., 2016a, b). Three different marine transgressions are known (Cabrera and Calvet, 1996; Roca et al., 1999; de Gibert and Casanovas-Vilar, 2011; Casanovas-Vilar et al., 2016a, b): the first is dated to the late Burdigalian and its sediments are mainly composed of evaporitic deposits; the second, and most extensive, is dated to the Langhian, and its sediments are formed by detritic units at the NE, associated to coastal enviroments, and carbonatic units at the SW, associated with a shallow marine platform; and the last transgression is dated to the Serravallian, and its sediments are formed mainly by carbonatic layers oiriginated at the marine platform.

Upper Continental Complexes: This complex is formed mainly by continental deposits similar in lithology to those of the lower continental complex. This continental sedimentation started at the early Serravallian (late Aragonian) and ended at the Tortonian (middle Turolian). This large period of sedimentation was caused by the reactivation of the Vallès-Penedès main fault, and provoked the development of large alluvial fan systems that came from the Prelittoral range (Cabrera and Calvet, 1996; Garcés et al., 1996; Roca et al., 1999; Casanovas-Vilar et al., 2008; de Gibert and Casanovas-Vilar, 2011; Casanovas-Vilar et al., 2016a, b). The sedimentation was interrupted at the end of the Miocene due to the late Messinian sea level fall (Cabrera and Calvet, 1996).

Pliocene, Pleistocene and Holocene sediments can also be found scattered through the Vallès-Penedès Basin (Martinell, 1988; Berástegui et al., 2000). The Pliocene deposits are associated with detritic units, corresponding to alluvial and fluvial enviroments, and detritic and carbonatic units, corresponding to shallow marine sedimentation. The Pleistocene and Holocene deposits are mainly formed by alluvial and colluvial units, with origin at both limiting mountain ranges.

Geologically, most of the documented vertebrate fossil sites are located in distal or marginal facies of the alluvial fan systems and are dominated by mudstones (Fig. 2), although some karstic sites are also known.

Paleontologically, the basin has been studied for decades, resulting in a particularly well known late Aragonian and Vallesian record of terrestrial mammals (Berástegui et al., 2000; Berástegui and Losantos, 2001; Madurell-Malapeira et al., 2010, 2017; Casanovas-Vilar et al., 2011, 2016a). Some of the fossils studied in this dissertation come from three sites of this basin (Casanovas-Vilar et al., 2016a): Ronda Oest de Sabadell (Sabadell, MN10) and Torrentet dels Traginers (Piera, MN12), corresponding to the upper continental complex; and the Vallparadís Section (Terrassa, Early to Middle Pleistocene), situated in one of the Pleistocene alluvial fans (Berástegui et al., 2000).

2.1.1. Ronda Oest de Sabadell

The fossil site of Ronda Oest de Sabadell (ROS) was discovered in 2009 during the paleontological surveillance of the construction of a road near the city of Sabadell (Madurell-Malapeira et al., 2014a; Casanovas-Vilar et al., 2016a, b; see also chapter 4). The majority of the 1200 remains recovered from the surveillance came from the following localities (Blaya Martí et al., 2012): ROS-A1, ROS-D1, ROS-D2, ROS-D3, ROS-D4, ROS-D5, ROS-D6, ROS-D7, ROS-D8. According to biostratigraphic data, ROS localities cover a time span ranging from the late Vallesian (MN10) to the early Turolian (MN11; Blaya Martí et al., 2012; Madurell-Malapeira et al., 2014a; Casanovas-Vilar et al., 2016a, b). The faunal list includes more than 30 species, most of them corresponding to large mammals (Blaya Martí et al., 2012; Madurell-Malapeira et al., 2014a): *Deinotherium giganteum*, Gomphoteriidae indet., Chalicotheriidae indet, Rhinocerontidae indet., Suidae indet., *Hippotherium* sp., *Mycromeryx* sp., *Euprox* sp., *Tragoportax* sp., Mustelidae indet., *Machairodus aphanistus* and *Hyaenictis* aff. *almerai*. The micrommal assemblage includes the murids *Progonomys cathalai* and *Parapodemus* sp. nov., and the cricetids *Kowalskia ambarrensis* and *Rotundomys* cf. *montisrotundi.*

2.1.2. Torrentet dels Traginers

This site, frequently grouped with others under the common denomination of Piera in the paleontological literature (e.g., Agustí et al., 1985; Morales et al., 1999), is placed in the surroundings of the town of Piera. The sediments around Piera correspond to the Torrelles de

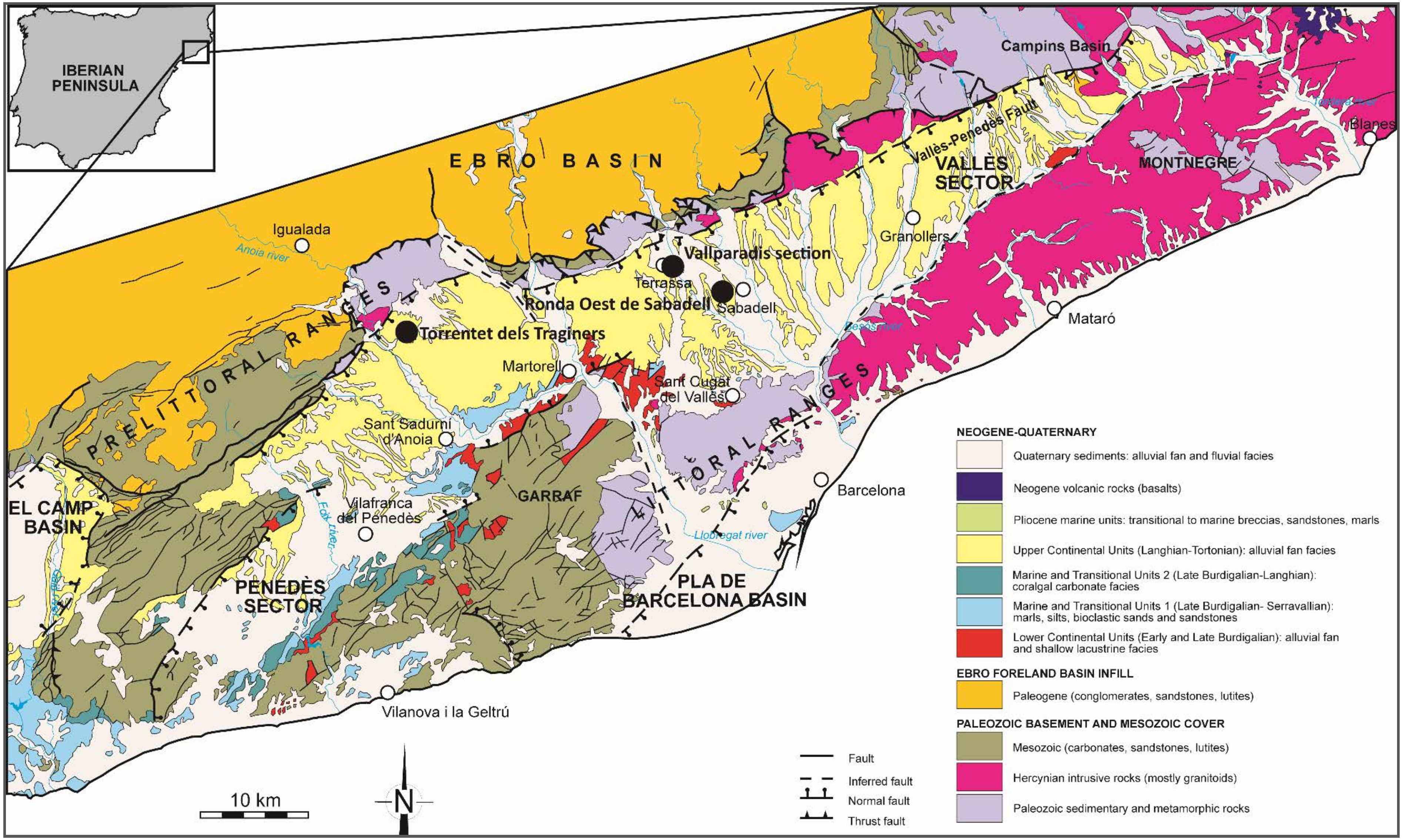

Figure 2.1: Geographic location of the Vallès-Penedès Basin within the Iberian Peninsula (top left inset) and schematic geological map of the basin. The three sites from where the studied material comes from are marked with black dots in the map (modified from Casanovas-Vilar et al., 2016a).

Foix alluvial system, being mainly formed by reddish mudstones, with embedded conglomerates (Roca and Muñoz, 2010); the fossils are placed with high density within a cemented breccia within the sequence (Villalta Comella and Crusafont Pairó, 1948; Crusafont Pairó, 1952). The main fossiliferous level was discovered by a neighbor of Piera in 1936, and the first known remains were recovered and sold to Crusafont Pairó and Villalta Comella in 1942, which immediately began the excavations of the site, which terminated in 1945. The recovered fossils were described in several publications (Villalta Comella and Crusafont Pairó, 1943, 1946, 1948; Crusafont Pairó, 1952). The site was not excavated further until 1980, when Moyà-Solà recovered new fossil remains from the site and micromammal samplings were taken (Moyà-Solà, 1983; Agustí et al., 1985; Casanovas-Vilar et al., 2016b). Despite the former publications and others subsequent ones (Crusafont Pairó and Aguirre, 1972; Santafé-Llopis and Casanovas-Cladellas, 1982; García Fernandez and Cerdeño, 1989), the large mammal assemblage has been poorly studied in detail. It includes *Tragoportax gaudryi*, *Cremohipparion mediterraneum*, *Birgerbohlinia schaubi*, *Microstonyx major*, *Anisodon* sp., *Aceratherium* sp., *Dihoplus* sp., *Stenailurus* sp., and *Adcrocuta eximia*. This site has long been dated to MN11 due to its macromammal association (Agustí et al., 1985, 1997; Van der Made et al., 1992; Casanovas-Vilar et al., 2011), but the few remains of micromammals, which include the murid *Occitanomys adroveri*, suggests an MN12 age for the site (Casanovas-Vilar et al., 2016b).

2.1.3. Vallparadís Section

The Vallparadís Section is located within the city of Terrassa (Barcelona, Spain). The deposits where the fossils where unearthed correspond to the Pleistocene alluvial fan system of Terrassa (Berástegui et al., 2000; Berástegui and Losantos, 2001; Madurell-Malapeira et al., 2010, 2017; see also chapter 7), which lie over the marked Miocene paleorelief of the area. The section has two main sites, one on each side of the Vallparadis torrent, that were discovered during construction works: Cal Guardiola in the west, during the construction of a sociosanitary building in 1997 (Berástegui et al., 2000); and Vallparadis Estació in the east, during the construction of a train station in 2005-2008 (Madurell-Malapeira et al., 2010, 2017). The Cal Guardiola local section is mainly formed by conglomerates, but the fossils are mainly confined to a black level embedded within them (Berástegui et al., 2000). The Vallparadis Estació local section is divided into two mayor units, which are also formed mainly by conglomerates and gravels, intercalated with mudstones (Madurell-Malapeira et al., 2010, 2017). The fossils in Vallparadis Estació are mainly located in 3 different layers of the sequence, EVT3, EVT7 and EVT12 (Madurell-Malapeira et al., 2010). The recorded species in the late Early Pleistocene layers are *Ursus deningeri*, *Pachycrocuta brevirostris*, *Homotherium latidens*, *Megantereon whitei, Panthera gombaszoegensis*, *Puma pardoides*, *Lynx pardinus*, Felidae indet. (large form), *Lycaon lycaonoides, Canis mosbachensis*, *Vulpes praeglacialis*, *Meles meles avatus*, *Mammuthus* sp., *Hippopotamus antiquus*, *Bison* sp., Bovidae indet., Caprini indet., *Megaloceros savini*, *Dama vallonnetensis*, *Stephanorhinus hundsheimensis*, *Equus altidens*, *Macaca sylvanus* cf. *florentina*, *Apodemus* cf. *sylvaticus*, *Stenocranius gregaloides*, *Iberomys huescarensis*, *Eliomys quericinus*, *Mimomys savini* and *Hystrix refossa* (Madurell-Malapeira et al., 2010, 2017; Madurell-Malapeira pers. comm. 2018; see also chapter 7). The different layers of both sites have been dated trough different methods, such as magnetostratigraphy and biostratigraphy of small mammals corresponding to ca. 1.2-0.6 Ma (Berástegui et al., 2000; Postigo Mijarra et al., 2007; Madurell-Malapeira et al., 2010).

2.2. Other sites

The sites considered below are located outside the Vallès-Penedès Basin (Fig 2.2). Three are located elsewhere in the Iberian Peninsula, such as Villarroya (Logroño), La Puebla de Valverde (Teruel), or Cueva Victoria (Murcia), whereas others come from other regions of Eurasia, such as Cava Nuzzo (Italy) and The Lingxiandong cave (China)

Figure 2.2: Geographic position of the sites placed outside of the Vallès-Penedès Basin.

2.2.1. Villarroya

The site of Villarroya is located in the northern Spanish region of La Rioja, in the boundary between the Ebro and Cameros basins. The Cameros Basin is formed mainly by

Mesozoic and Cenozoic rocks, while the Ebro Basin is formed mainly by Cenozoic and Quaternary materials (Muñoz et al., 2016). The fossil site is placed inside a small Pliocene patch of sediments that crops out in the area, about 12 km^2 in width and 200 m in thickness. The boundaries of this Pliocene section are only well defined at the east and the south, being surrounded by Quaternary alluvial terraces very similar in appearance, while its lower boundary is discordant with the Weald Facies, except in the north, where it is concordant (Villalta, 1952; Fernández de Bobadilla 1963a, b, 1964a, b; Muñoz et al., 2016). The Pliocene unit is composed of white sandstones, a red alternation of shale/sands and conglomerates, and some limestone beds at the top (Villalta, 1952; Muñoz et al., 2016). The fossiliferous level is located in 2 m of red shale in the middle alternation of shale and sands. The fossils are disposed in high density bags, usually well preserved and unbroken, and even a few are preserved in anatomical connection. Villalta (1952) interpreted the accumulation as indicating short transport of the remains, within the depositional environment consisting of a small endorheic basin with several small seasonal lakes, in which the bones were buried at the bottom, free to be altered by scavengers or the weather. The recent stratigraphical study generally supported this interpretation but rejected the seasonal character of the lake (Muñoz et al., 2016)

After its discovery by Carvajal (1926), several field campaigns have been performed at Villarroya, including those executed in the 1950s by M. Crusafont-Pairó and J.F. de Villalta, or the last ones in the 1990s led by S. Jiménez García. The publications about the site always followed these campaigns (Villalta, 1952; Fernandez de Bobadilla, 1963a, b, 1964a, b; Jiménez et al., 1999), and despite previous debates about its age, it is now considered a classic site of the early Villafranchian close to the Plio-Pleistocene boundary (2.6 Ma; Pueyo et al., 2016; Laplana et al., 2016). Up to 20 species of large mammals have been identified: *Homotherium latidens*, *Megantereon cultridens*, *Acinonyx pardiensis*, *Lynx issidorensis*, *Pliocrocuta perrieri*, *Chasmaporthetes lunensis*, *Ursus etruscus*, *Nyctereutes megamastoides*, *Vulpes alopecoides*, *Enhydrictis ardea*, *Anancus arvernensis*, *Arvernoceros ardei*, *Croizetocerus ramosus*, *Praeelaphus perrieri*, *Megalovis* sp., *Gazella borbonica*, *Gazellospira torticornis*, *Leptobos elatus*, *Hesperioceras merlae*, *Hipparion rocinantis* and *Stephanorinus etruscus* (Madurell-Malapeira et al., 2014b; Andrés et al., 2016; Cerdeño and Alberdi, 2016; Morales, 2016) The fossils collected from the various campaigns are housed in several collections troughout Spain.

2.2.2. La Puebla de Valverde

La Puebla de Valverde is located in the Sarrión-Mijares depression within the Teruel Basin (eastern Iberian Peninsula; Gautier and Heintz, 1974). It was considered one of the classical Pliocene sites of Europe, although is is currently dated to the Early Pleistocene, given that the Pliocene-Pleistocene boundary was transferred to 2.6 Ma. It was discovered in 1962 by D. Pascual Plumed (Andrés Rodrigo, 2011) and posteriorly excavated by Heintz and Crusafont, who also published the first known description of the site (Crusafont et al., 1964). More field campaigns took place in the 1960s and 1970s, and the site was not excavated further 1998, when fieldwork was resumed (Aguirre and Soto, 1974; 1978; Heintz and Aguirre, 1976; Heintz, 1978; Andrés Rodrigo, 2011). The Early Pleistocene patch is placed in discordance with the Mesozoic materials and has two units, the Sarrión Formation and La Puebla de Valverde Formation, which are separated by an erosive surface (Crusafont et al., 1964; Gautier and Heintz, 1974; Adrover et al., 1974; Sinusía et al., 2004; Andrés Rodrigo, 2011). The first, where the fossils are found, is composed of reddish sandstones and clays with intercalations of conglomerate channels, whereas the second is similar, but with yellowish materials and less developed conglomerates (Crusafont et al., 1964; Gautier and Heintz, 1974; Adrover et al., 1974; Sinusía et al., 2004). The site is dated to MN17 or middle Villafranchian according to the faunal list, which includes 23 species of macromammals: *Paradolichopithecus* aff. *arvernensis*, *Mammuthus meridionalis*, *Equus stenonis*, *Stephanorhinus etruscus*, *Gazellospira torticornis*, *Gazella borbonica*, *Gallogoral menehinii*, *Eucladoceros senezensis*, *Cervus philisi*, *Croizetoceros ramosus*, *Lycaon* cf. *falconeri*, *Vulpes alopecoides*, *Nyctereutes megamastoides*, *Ursus etruscus*, *Pliocrocuta perrieri*, *Chasmaporthetes lunensis*, *Lynx issidorensis*, *Puma pardoides*, *Acinonyx pardinensis*, *Megantereon cultridens* and *Homotherium latidens* (Andrés Rodrigo, 2011; Madurell-Malapeira et al., 2010, 2014b). The magnetostratigraphic analysis yields an estimated age of 2.14–1.95 Ma (Sinusía et al., 2004), which agrees well with previously estimated dates based on the micromammal fauna (Crusafont et al., 1964; Gautier and Heintz, 1974; Adrover et al., 1974). Thanks to the good preservation of the fossils, many works have focused on the remains from this site (Heintz, 1970, 1978; Heintz et al., 1971; Aguirre and Soto, 1974, 1978; Heintz and Aguirre, 1976; Alberdi et al., 1997; Antón et al., 2006; Andrés-Rodrigo, 2011).

2.2.3. Cueva Victoria

The karstic site of Cueva Victoria is situated southeastern within the Iberian Peninsula, more precisely in the town of La Unión (Murcia, Spain). The cave itself, located in a hill nearby the town, has up to 3 km of horizontal galleries, although the fossil layers are located close to the cave entrances. It was discovered in the early 1970 (Valenzuela, 1970) due to both its minerals and fossil remains. Historically, the area was heavily mined during the end of the 19th and the beginning of the 20th centuries, in order to extract the deposits rich in iron and manganese minerals present in the area (Pérez de Perceval et al., 2015). The cave was probably formed during the Pliocene, as a karstic complex within the Triassic limestone outcrops present in the area (Ferrández-Cañadell, 2015). The cave was probably filled during the late Early Pleistocene (0.9–0.8 Ma; Martín, 2012; Gibert and Scott, 2015) and the recovered fossil remains were supposedly carried inside by large hyenas of the species *Pachycrocuta brevirostris* (Gibert et al., 1992, 1993). After the sealing of the cave entrances, the cave was emptied in the mining works; the fossil remains found subsequently are located in the untouched original filling layers of the cave. After its rediscovery, there have been several digging campaigns over the years, from 1984 until 2011, to extract the fossil remains from the untouched levels and the wastes of the mining works (Ferrández-Cañadell and Gibert, 2015). There have been several studies of the fauna present in the cave throughout the years, initially focused on carnivorans (Pons-Moyà and Moyà-Solà, 1978; Pons-Moyà, 1981, 1982, 1983) and the presence of human remains (Carbonell et al., 1981; Pons-Moyà, 1982; 1985). Most recently, a monograph summarizing all the available information was published (Ferrández-Cañadell and Gibert, 2015). The current faunal list identifies up to 24 macromammal species (hominids excluded): *Equus altidens*, *Equus suessenbornensis*, *Stephanorhinus* aff. *etruscus*, *Hemitragus bonali*, *Praeovibos priscus*, *Ovis antiqua*, Ovibovini indet., *Bison* sp., *Megaloceros novocarthaginiensis*, *Dama* cf. *vallonnetensis*, *Mammuthus* cf. *meridionalis*, *Homotherium latidens*, *Megantereon* sp., *Panthera gombaszoegensis*, *Puma pardoides*, *Lynx pardinus*, *Ursus deningeri*, *Pachycrocuta brevirostris*, *Canis mosbachensis*, *Lycaon lycanoides*, *Vulpes* sp., *Mustela* sp., and *Monachus* sp. (Madurell-Malapeira et al., 2014b, 2015; Ferrández-Cañadell and Gibert, 2015).

2.2.4. Cava Nuzzo

Little is known about this site based on the published literature, with only a single paper detailing with its geology and faunal association (Bologna et al., 1994). The site of Cava

Nuzzo is located on the Melpignano area (Lecce, Italy), were many Quaternary (Middle-Late Pleistocene) deposits are found. There are different kind of deposits in this area, with the site corresponding with a certain type of karst infill called "ventarole". The site itself is situated in one of the many quarries that extract the "Pietra Leccesse", called Cava Nuzzo. The ventarole are karst cavities in Miocene calcarenite filled with reddish sediments full of vertebrate remains. These remains are along all the thickness of the deposit, without preferential orientation and showing low transportation, as they are very well preserved. Its genesis, with an unclear stratigraphic succession, makes its correlation hard since it has to rely entirely relies on the fauna assemblage. This faunal association, with the presence of the hominin *Homo* cf. *neanderthalensis*, limits the age of the sediments to the Late Pleistocene, more precisely to the MIS5c-5a or younger isotopic stages. The non-human macromammal assemblage includes *Palaeoloxodon* cf. *antiquus*, *Stephanorhinus* sp., *Equus caballus*, *Equus hydruntinus*, *Sus scrofa*, *Bison priscus*, *Bos primigenius*, *Cervus elaphus*, *Dama dama*, *Capreolus capreolus*, *Canis lupus*, *Vulpes vulpes*, *Lynx lynx*, *Crocuta crocuta*, and *Meles meles*.

2.2.5. Lingxiandong Cave

The Lingxiandong Cave (Liu et al., 2015) is located in the northeastern Hebei Province in China, in the northern margin of the Liujiang Mountains. Geologically, it belongs to the east section of the Yanshan basin of the North Chinese Platform. The carbonates of this region form different karstic systems, the site corresponding to one of them. It is a multilayered cave system formed due to the intermittent ascending motion of the Liujiang Basin. It is still active and has at least three layers connected vertically with a chimney or hole. These three layers are correlated also with the nearby terraces of the Shihe river. The main cavity was formed during the Huangshui erosion period (Liu et al., 2015), and the accumulation took place in the Zhokou period (Pleistocene; Liu et al., 2015). The deposits inside the cave are mainly clay and gravel. Fossils can be found in two areas within the cave; 27 species have been identified. The complete macromammal assemblage includes *Crocuta ultima*, *Canis lupus*, *Vulpes corsac*, *Stephanorhinus kirchbergensis* and *Cervus elaphus*. According to the micromammal and macromammal assemblage, the site is dated around late Middle to early Late Pleistocene (>50 ka; Sheng et al., 2014).

Chapter 3. Materials and methods

3.1. Studied sample

Most of the studied fossil remains are housed at the Institut Català de Paleontologia Miquel Crusafont (ICP), including the samples from Villarroya (IPS36758 and IPS36759), La Puebla de Valverde (IPS27340), Ronda Oest de Sabadell (IPS62078), Cueva Victoria (see complete list in chapter 6), the Vallparadís Section (see chapter 7), and Torrentet dels Traginers (IPS36523 and IPS8965, included in the appendix).

The material not housed at the ICP includes specimens from Cava Nuzzo (Italy) and Linxiandong cave (China). The Italian specimens (MPD13 and MPD15) are housed in the Earth Sciences Department of the Sapienza University in Rome, whereas the Chinese material (LXD007) is housed in the Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences in Beijing.

3.2. Comparative sample

Part of the comparative sample used in this dissertation has been directly measured (either physically or through a 3D model), but most of the data were taken from the literature. The directly measured material includes specimens from the following species: *Hyaenictis almerai* from Sant Miquel de Toudell (housed at the Museu de Ciències Naturals de Barcelona, Barcelona, Spain), *Adcrocuta eximia* from Torrentet dels Traginers (housed at the ICP), *Chasmaporthetes lunensis* from La Puebla de Valverde (housed at the Museo Nacional de Ciencias Naturales-CSIC, Madrid), and *Hyaenictis hendeyi* from Langenbaanweg (housed at the South African Museum, Cape Town, South Africa).

The comparative sample based 3D models consists of CT-scans of hyaenid skulls (see section 1.4.5) that were kindly provided by the Digimorph Team (www. digimorph.org). They include a skull of *Crocuta crocuta* (MVZ 184551) and a skull of *Parahyaena brunnea* (MVZ 117842) housed at the University of California in Berkeley (California, USA), as well as a skull of *Hyaena hyaena* (USNM 182034) housed at the National Museum of Natural History (Washington, DC, USA).

The comparative sample taken from the literature (Gaudry, 1861; Villalta Comella and Crusafont Pairó, 1948; Viret, 1954; Adrover and Soria, 1976; Hendey, 1978; Howell and Petter, 1980, 1985; Qiu, 1987; Kurtén and Werdelin, 1988; Werdelin, 1988, 1999; Geraads, 1997; Turner, 2001; Argant, 2004; Baryshnikov and Tsoukala, 2010; Koufos, 2011; Werdelin and Lewis, 2012; Tseng et al., 2013) includes specimens from almost all large extinct hyaenid genera: *Pliocrocuta*, *Pachycrocuta*, *Chasmaporthetes*, *Hyaenictis*, *Lycyaena* and *Lycyaenops.*

For further details on the comparative samples used in each paper, see the respective subsection in chapters 4–10.

3.3. Computed tomography

The CT-scans used in this dissertation were taken in different institutions with different parameters. The first *Pliocrocuta perrieri* skull (IPS36759) was scanned at the Mútua de Terrassa hospital (Terrassa), using a Siemens Sensation 16 at 140 kV and 300 mA. The remaining *Pliocrocuta* specimens (IPS36758 and IPS27340), as well as the *Adcrocuta* sample (IPS36523 and IPS8965), were scanned at the ICP using an industrial CT scanner YXLON Y.TU 450-D09, at 350 kV and 2 mA for IPS36758, 430 kV and 3 mA for IPS27340, 400 kV and 3.75 mA for IPS36523, and 350 kV and 4.25 mA for IPS8965. The specimens of *Crocuta spelaea* from Italy (MPD15 and MPD13) were scanned using a Philips Brilliance CT 64-channel scanner at M. G. Vannini Hospital (Rome), at 120 kV and 500 mA. The Chinese specimen of *Crocuta ultima* (LDX007) was scanned at the Key Laboratory of Vertebrate Evolution and Human Origins using microcomputerized tomography developed by the Institute of High Energy Physics, Chinese Academy of Sciences (CAS), at 430 kV and 1.5 mA. The crania of extant taxa were scanned at the University of Texas High-Resolution X-ray Computed Tomography Facility – Digital Morphology Group using an ACTIS CT scanner. For detailed scan parameters of the extinct specimens see chapters 9 and 10; and for further information about the scan parameters used in the extant specimens, visit http://www.digimorph.org. The 3D virtual models of the cranium and the endocranial cavities were derived from the CT-scans using Hounsfield units as reference units. Segmentation and 3D rendering of the specimens were done using Avizo 7.0 (FEI-VSG, France). This software was also used to generate the 3D surfaces and volumes using the same steps for each CT-scan.

3.4. Measurements, anatomical nomenclature and statistics

The anatomical and osteological terminology used in the descriptions follow Evans and de Lahunta (2013; Fig. 4.1). Dental terminology follows Werdelin and Solounias (1991; Fig. 4.2), whereas brain morphology terminology follows Sakai et al. (2011). Craniomandibular and dental measurements of the studied specimens were taken with digital calipers to the nearest 0.1 mm.

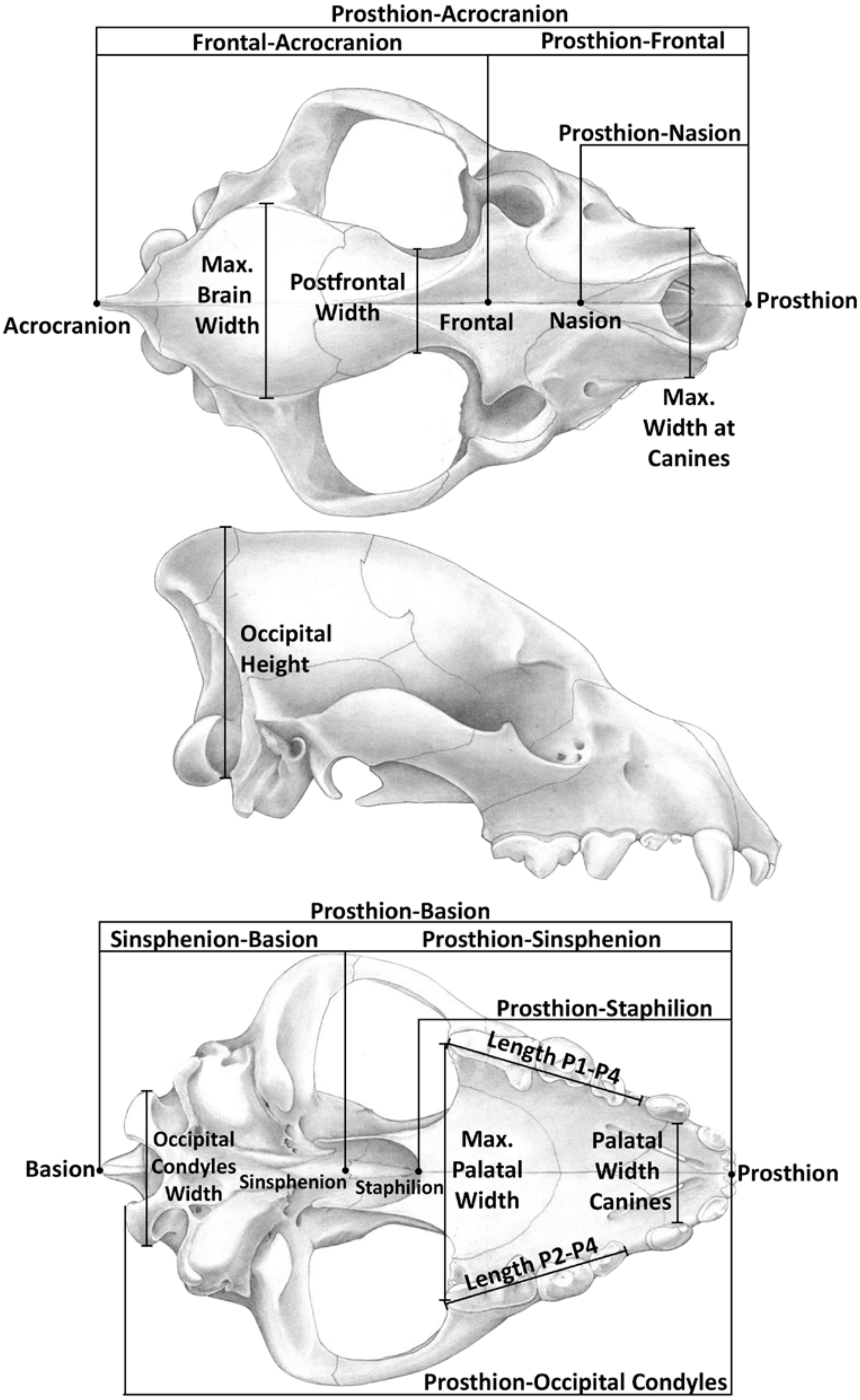

Figure 3.1: Detailed cranial measurements used in this work (modified from Werdelin and Solounias, 1991).

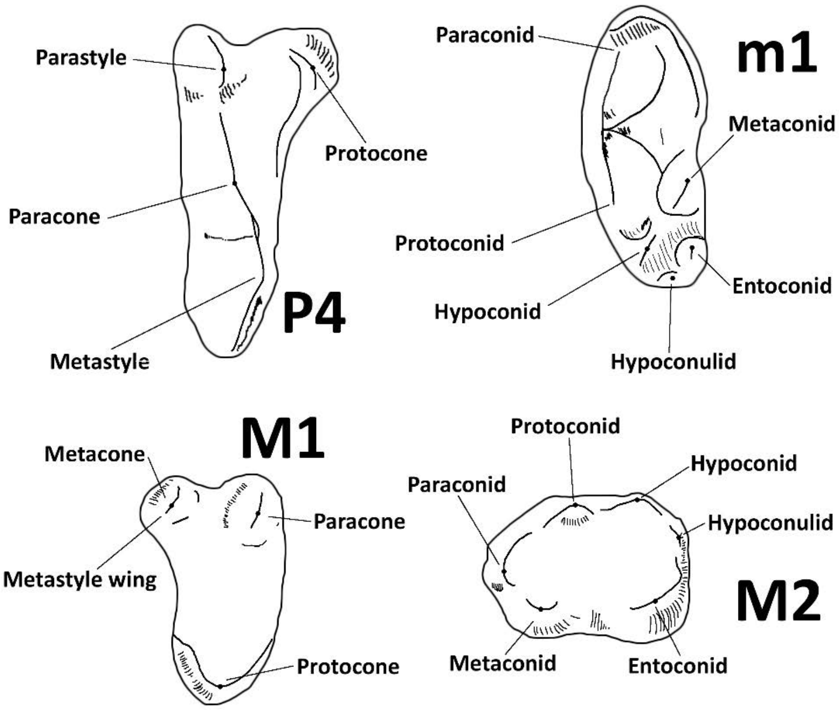

Figure 3.2: Dental nomenclature used in this dissertation (modified from Werdelin and Solounias, 1991).

Total and regional brain volumes were measured for all specimens with Rhinoceros 5.0 (McNeel, USA). Regional brain volumes were measured in agreement with previous literature (Arsznov et al., 2010; Sakai et al., 2011; Swanson et al., 2012), by subdividing virtual endocasts into the following three regions, based on sulcal patterns and/or bony landmarks: anterior cerebrum, posterior cerebrum, and cerebellum plus brain stem (Fig. 4.3; see chapters 9 and 10 for further details). To compute regional brain volumes in the fossil specimens, following Sakai et al. (2011) we relied on a ratio of the volume of each region relative to total brain cavity volume (which includes the olfactory bulbs, the cerebrum, the cerebellum and the brain stem.

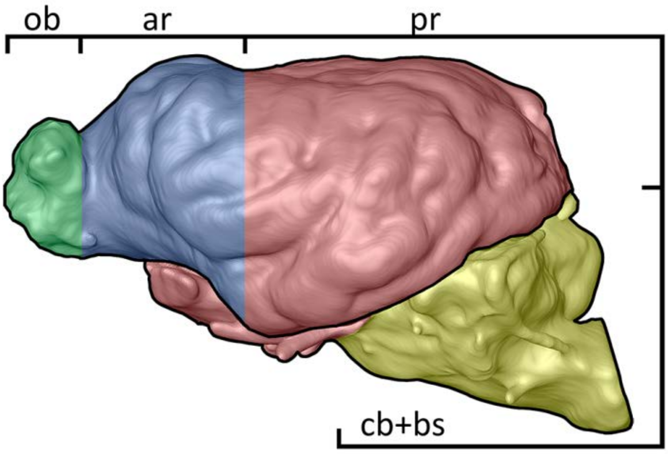

Figure 3.3: Regional division of the brain according to Sakai et al. (2011). Image taken from chapter 10.

The abbreviations used for craniodental measures are reported in Table 3.1, and those used for brain regions and sulci are provided in Table 3.2.

Statistical analyses in this dissertation have been performed using IBM SPSS Statistics v. 19, v. 20 and the free software PAST v2.15 (Hammer et al., 2001). They include bivariate plots, box-and-whisker plots, linear regressions, principal components analysis (PCA), analysis of variance (ANOVA) and discriminant analysis (DA). See chapters 4–10 for further details.

Table 3.1: Complete list of abbreviations for craniodental measures used in this dissertation.

Craniodental measure	Abbreviation
buccolingual breadth	B
breadth/length index	BLI
frontal-acrocranion	FA
frontal-acrocranion length	FA
occipital height	Hoc
mesiodistal length	L
length of the upper premolar series	LP1–P4
mesiodistal length of P4 metastyle	LP4m
mesiodistal length of fourth upper premolar paracone	LP4pa
mesiodistal length of fourth upper premolar parastyle	LP4pas
mesiodistal length of fourth upper premolar protocone	LP4pr
mesiodistal length of the m1 talonid	Ltm1
prosthion-acrocranion length	PA
prosthion-basion length	PB
prosthion-frontal length	PF
prosthion-nasion length	PN
prosthion-sinsphenion length	PS
prosthion-staphilion length	PST, PT
synsphenion-basion length	SB
prosthion-occipital condyle length	SKL
palatal width at C1	WC
palatal width at P4	WiP4
width of occipital condyles	Woc
palatal width at P4	WP4

Table 3.2: Complete list of abbreviations used in the descriptions of the brain morphology in this dissertation.

Brain feature	Abbreviation
ansate sulcus	a
anterior cebrebrum region	ar
coronal sulcus	c
cerebellum plus brain stem region	cb+bs
cruciate sulcus	cr
ectolateral sulcus	el
ectosylvian sulcus	es
lateral sulcus	l
longitudinal fissure	lf
olfactory bulbs	ob
precruciate gyrus	pg
posterior cerebrum region	pr
proreal sulcus	prs
presylvian sulcus	ps
sylvian sulcus	s
suprasylvian sulcus	ss

Chapter 4. A new skull of *Hyaenictis* Gaudry, 1861 (Carnivora, Hyaenidae) shows incipient adaptations to durophagy

Reference: Vinuesa, V., Madurell-Malapeira, J., Werdelin, L., Robles, J.M., Obradó, P., & Alba, D.M. (2017). A new skull of *Hyaenictis* Gaudry, 1861 (Carnivora, Hyaenidae) shows incipient adaptations to durophagy. *Journal of Mammalian Evolution 24*, 207–219.

Summary: This work describes and compares new material (a skull and two hemimandibles) of one of the least known extinct hyaenid genera, *Hyaenictis*. The material is compared morphometrically to several species of this genus as well as other genera.

Author's contribution: The doctoral candidate is the first author and was involved in all stages of the study, including the description of the specimens, the statistical analyses and the writing of the manuscript.

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ORIGINAL PAPER

A New Skull of *Hyaenictis* Gaudry, 1861 (Carnivora, Hyaenidae) Shows Incipient Adaptations to Durophagy

Víctor Vinuesa[1] **· Joan Madurell-Malapeira**[1] **· Lars Werdelin**[2] **· Josep M. Robles**[1] **·**
Pau Obradó[1] **· David M. Alba**[1]

Abstract The European Miocene records a wide diversity of hyaenid ecomorphotypes represented by multiple genera. Among these, *Hyaenictis* Gaudry, 1861, is one of the least known. This genus includes four species from the late Miocene and Pliocene of the Old World, but in Europe *Hyaenictis* is only represented by two species, recorded by scarce and fragmentary remains: *Hyaenictis graeca* Gaudry, 1861, from Pikermi (MN12; Greece) and *Hyaenictis almerai* Villalta Comella and Crusafont Pairó, 1948, from Sant Miquel de Toudell (MN10; Vallès-Penedès Basin, NE Iberia). Here, we describe a new skull of *Hyaenictis* aff. *almerai* from the Vallès-Penedès site of Ronda Oest Sabadell Sector D (MN10), representing the most complete European specimen of the genus. In the presence of m2 and virtual lack of m1 metaconid, the described cranium more closely resembles *Hyaenictis* rather than any other medium- to large-sized European hyaenid. However, the new skull does not fit well with previously known *Hyaenictis* species, more closely resembling the bone-cracking *Adcrocuta* Kretzoi, 1938, in the development of premolar accessory cuspids and the possession of relatively broad cheek teeth. These and other features (strong mandibular muscular insertions and enamel microstructure) denote more durophagous adaptations than previously documented in *Hyaenictis* (considered a cursorial/dog-like hyaena), and favor the inclusion of *H.* aff. *almerai* in the transitional bone-cracking hyaenid ecomorphotype.

Keywords Fossil carnivorans · Miocene hyaenids · Bone-cracking hyenas · Taxonomy · Vallesian · NE Iberian Peninsula

Introduction

The Genus *Hyaenictis*

Hyaenictis Gaudry, 1861, and its type species, *Hyaenictis graeca* Gaudry, 1861, were erected on the basis of scarce dentognathic remains from the Greek locality of Pikermi (MN12, middle Turolian, late Miocene). The holotype is a juvenile hemimandible with dc, p1 alveolus, dp2–dp4, erupting m1 and m2, and exposed p2-p4 inside their crypts. A few additional dentognathic remains, including two juvenile maxillary fragments, have been further attributed to the same taxon (see also Howell and Petter 1985; Werdelin et al. 1994; Koufos 2011). This species is characterized by a mixture of primitive features (retention of p1 and m2) and several derived traits (such as vestigial m1 metaconid; Gaudry 1861; Howell and Petter 1985; Werdelin et al. 1994). An adult partial hemimandible of this genus was found in 1920 in the Iberian locality of Sant Miquel de Toudell (SMT; formerly spelled 'Taudell') in the area of Viladecavalls (Vallès-Penedès Basin; MN10, late Vallesian, late Miocene). This specimen was initially attributed to *H. graeca* by Bataller (1921; see also Villalta Comella and Crusafont Pairó 1941, 1943), but later designated as the holotype of another species of the genus, *Hyaenictis almerai* Villalta Comella and Crusafont Pairó, 1948. According to Villalta Comella and Crusafont Pairó (1948), *H. almerai* resembles *H. graeca* in the retention of m2 and the lack of m1 metaconid, but differs from it in several other features (shorter and stouter mandibular corpus, shorter diastema, and apparent lack of p1).

✉ David M. Alba
david.m.alba@gmail.com

[1] Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, Carrer de les Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain

[2] Department of Palaeobiology, Swedish Museum of Natural History, Box 50007, S-10405 Stockholm, Sweden

Solounias (1981) synonymized *Adcrocuta* Kretzoi, 1938, with *Hyaenictis* based on similarities in the m1 and the lack of additional remains of *H. graeca* among the vast hyaenid sample from Pikermi. However, this taxonomic opinion was discounted by subsequent authors (Howell and Petter 1985; Werdelin and Solounias 1990, 1991). Werdelin and Solounias (1991) noted that only a few similarities justified the attribution of the hyaenid from Sant Miquel de Toudell to *Hyaenictis*, but tentatively retained this generic assignment, in spite of recognizing that the erection of a new genus might eventually be justified. Later, *Hyaenictis hendeyi* Werdelin et al. 1994, was erected based on early Pliocene (ca. 5 Ma) material from Langebaanweg in South Africa, previously attributed to indeterminate species of *Euryboas* Schaub, 1941 (Hendey 1976, 1978). Some additional middle Miocene to early Pliocene hyaenid remains from elsewhere in Africa have been subsequently attributed to *Hyaenictis*. These specimens are mostly isolated teeth (Ginsburg 1977; Turner 1988; Morales et al. 2005; Werdelin and Peigné 2010). The exception is *Hyaenictis wehaietu* Haile-Selassie and Howell, 2009, from the late Miocene and early Pliocene of the Middle Awash in Ethiopia (5.8–5.2 Ma), which is represented by more abundant material (Haile-Selassie and Howell 2009). Besides its smaller size, this species differs from *H. graeca* by the lack of p1 and m2, and the presence of a well-developed m1 metaconid (Haile-Selassie and Howell 2009). Given the lack of these diagnostic features of the type species of the genus, the inclusion of this species in *Hyaenictis* is questionable (being here referred to as ?*Hyaenictis wehaietu*).

Hyaenictis has been classically included in the cursorial hyaenid ecomorphotype (Werdelin and Solounias 1996; Turner et al. 2008), given the lack of the typical durophagous adaptations of *Adcrocuta*. In this paper, we describe a new skull with associated mandible and atlas from the late Vallesian of the Vallès-Penedès Basin that, based on the retention of p1 and m2, as well as the reduced m1 metaconid, is attributed to *Hyaenictis*. This skull, which represents the most complete specimen of *Hyaenictis* known so far from the European Miocene, does not fit well with previously known species of this genus, from which it differs in several morphological and metric features that more closely resemble those of the bone-cracking hyaena *Adcrocuta*. The taxonomic assignment of the described specimen is discussed here, together with its implications for the evolution of durophagous adaptations in hyaenids during the late Miocene.

Age and Geological Background

The described material comes from sector ROS-D within the set of paleontological sites of Ronda Oest Sabadell (ROS), which were discovered between 2009 and 2011 during paleontological surveillance of the construction of a road near the city of Sabadell (Catalonia, Spain; Madurell-Malapeira et al. 2014). From a geological viewpoint, ROS is located within the Vallès-Penedès Basin (Fig. 1), a small and elongated half-graben oriented parallel to the Mediterranean coastline in the NE Iberian Peninsula and bounded by the Catalan (Prelittoral and Littoral) Coastal Ranges (Cabrera et al. 2004; de Gibert and Casanovas-Vilar 2011). This basin has been intensively sampled for many decades, resulting in a particularly well-known late Aragonian and Vallesian record of terrestrial mammals (Casanovas-Vilar et al. 2011, 2015). Based on biostratigraphic data, ROS localities cover a time span ranging from the late Vallesian (MN10) to the early Turolian (MN11; Madurell-Malapeira et al. 2014). The remains described here were found stratigraphically 1.5 m below locality ROS-D6, which on the basis of micromammals is correlated to the upper part of MN10 (Madurell-Malapeira et al. 2014; Casanovas-Vilar et al. 2015). More precisely, ROS-D6 is tentatively correlated to the *Rotundomys bressanus* local subzone of the Vallès-Penedès Basin (Casanovas-Vilar et al. 2015), with an estimated age of ca. 9.4–9.1 Ma, although alternatively it might, like SMT, belong to the older *Rotundomys montisrotundi* local subzone, which has an estimated age of 9.6–9.4 Ma (Casanovas-Vilar et al. 2015).

Materials and Methods

Studied Material and Comparative Sample

The hyaenid remains described in this paper are housed in the ICP (see institutional abbreviations below). Anatomical terminology used in the descriptions follows Evans and de Lahunta (2013). The examined fossil comparative sample includes the holotype (MGB16051) of *Hyaenictis almerai* from SMT (MN10), housed in the MCNB; remains of *Adrocuta eximia* Roth and Wagner, 1854, from Torrentet de Traginers (Piera, MN12), housed in the ICP; specimens of *Chasmaporthetes lunensis* (Del Campana, 1914) from La Puebla de Valverde (Teruel, MN17), housed in the MNCN; and topotypic specimens of *Hyaenictis hendeyi* housed in SAM. Additional data from other Miocene and Pliocene hyaenids included in the comparative sample were taken from the literature (Gaudry 1861; Villalta Comella and Crusafont Pairó 1948; Hendey 1978; Howell and Petter 1985; Qiu 1987; Kurtén and Werdelin 1988; Werdelin 1988, 1999; Koufos 2011; Tseng et al. 2013). They include: *Adcrocuta* (MN10–MN13, Eurasia), including *Adcrocuta eximia*; *Lycyaena* Hensel, 1863 (MN9–MN12, Eurasia and North Africa), including *Lycyaena chaeretis* (Gaudry, 1861), *Lycyaena dubia* Zdansky, 1924, and *Lycyaena crusafonti* Kurtén, 1976; *Chasmaporthetes* Hay, 1921 (MN12–early Pleistocene, Eurasia, Africa, and North America), including *Chasmaporthetes gangsriensis* Tseng et al., 2013, *Chasmaporthetes lunensis*, *Chasmaporthetes*

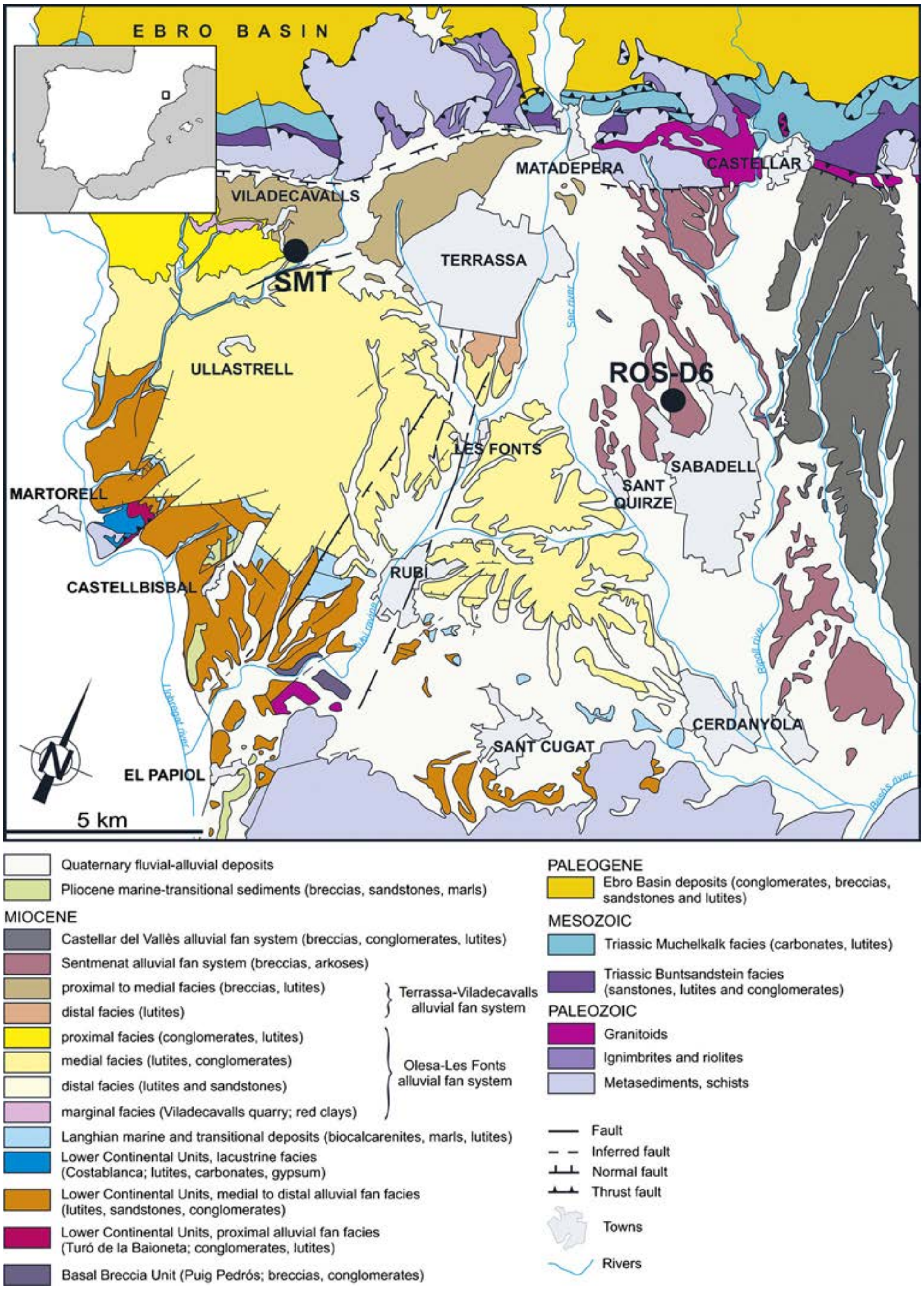

Fig. 1 Detailed geological map of the western (Vallès) sector of the Vallès-Penedès Basin (within the Iberian Peninsula), showing the position of the referred late Vallesian mammal sites (modified after Casanovas-Vilar et al. 2015). Locality acronyms: ROS-D, Ronda Oest Sabadell Sector D; SMT, Sant Miquel de Toudell

ossifragus Hay, 1921, *Chasmaporthetes borissiaki* (Khomenko, 1931), *Chasmaporthetes australis* (Hendey, 1974), and *Chasmaporthetes nitidula* (Ewer, 1955); *Lycyaenops* Kretzoi, 1938 (MN14–early Pleistocene, Europe and Africa), including *Lycyaenops silberbergi* (Broom in Broom and Schepers, 1946) and *Lycyaenops rhomboideae* Kretzoi, 1938; and *Hyaenictis* (MN10–MN14, Europe and Africa), including *H. graeca*, *H. almerai*, *H. hendeyi*, and ?*H. wehaietu*. The material of "*Chasmaporthetes*" *bonisi* Koufos, 1987, has been reassigned to *A. eximia* following Werdelin and Solounias (1991). The genera included in the comparative sample have been selected based on their age, geographic distribution, and morphological similarities with the ROS-D specimen.

Tooth Enamel Microstructure

Enamel microstructure (Hunter-Shreger Bands, HSB; Stefen 1997; Ferretti 1999, 2007) in the cheek teeth of the described material was described and photographed with a Leica MZ-16 light stereomicroscope with a Leica IC 3D digital camera attached. The resulting images were modified with the HDR (high dynamic range) toning function in Adobe Photoshop CS6 to enhance the contrast of the HSB.

Morphometric Comparisons

Craniomandibular and dental measurements of the studied specimens were taken with digital calipers to the nearest 0.1 mm (see measurement abbreviations below). Dental size and proportions were assessed using bivariate plots of buccolingual breadth (W) vs. mesiodistal length (L) for the lower cheek teeth (p2, p3, p4, and m1). A breadth/length index (BLI) for these teeth was computed as BLI = log (B/L), to assess differences in dental shape among the studied genera. These differences were inspected by means of boxplots and analysis of variance (ANOVA), including pairwise post-hoc comparisons (Bonferroni method), using IBM SPSS Statistics v. 19. A principal component analysis (PCA) based on the BLI of individuals preserving the p2–m1 series was performed with PAST v. 2.15 (Hammer et al. 2001). Note that the PCA (like ANOVA) was run on log-transformed data, so as to mini-mized the statistical problems associated with the usually non-normal distribution of ratios (although PCA makes no assumptions in this regard, it usually yields better results with normally distributed data; Hammer and Harper 2006). No statistical analyses were undertaken on the basis of the upper dentition, because of the scarcity of sufficiently complete cranial remains for most of the taxa included in the comparative sample (including *Hyaenictis* spp.). ?*Hyaenictis wehaietu* was not included in the morphometric comparisons (boxplots, ANOVA, and PCA), because as noted above this species is unlikely to belong to the genus *Hyaenictis*.

Abbreviations

Institutional Abbreviations ICP: Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona (Spain); IPS: acronym of the collections of the ICP (formerly Institut de Paleontologia de Sabadell). MCNB, Museu de Ciències Naturals de Barcelona (Spain); MGB: acronym of the geology collections of the MCNB (including the former Museu de Geologia de Barcelona); MNCN: Museo Nacional de Ciencias Naturales–CSIC, Madrid (Spain); MNHN: Muséum National d'Histoire Naturelle, Paris (France); SAM: Iziko South African Museum, Cape Town (South Africa).

Locality Abbreviations PIK: Pikermi; PQ-L: Pelletal Phosphorite and Quartzose Sand Members undifferentiated, Varswater Formation, "E" Quarry, Langebaanweg; ROS: Ronda Oest Sabadell; SMT: San Miquel de Toudell.

Measurement Abbreviations B: buccolingual breadth; BLI: breadth/length index; FA: frontal-acrocranion length; LP1–P4: length of the upper premolar series; PA: prosthion-acrocranion length; Hoc: occipital height; PB: prosthion-basion length; L: mesiodistal length; LP4m: mesiodistal length of P4 metastyle; LP4pa: mesiodistal length of fourth upper premolar paracone; LP4pas: mesiodistal length of fourth upper premolar parastyle; Ltm1: mesiodistal length of the m1 talonid; PF: prosthion-frontal length; PN: prosthion-nasion length; PS, prosthion-synsphenion length; PST: prosthion-staphylion length; SB: synsphenion-basion length; SKL: prosthion-occipital condyle length; WC: palatal width at C1; WiP4: palatal width at P4; Woc: width of occipital condyles.

Systematic Paleontology

Order **CARNIVORA** Bowdich, 1821
Suborder **FELIFORMIA** Kretzoi, 1945
Family **HYAENIDAE** Gray, 1821
Subfamily **HYAENINAE** Gray, 1821

Genus ***HYAENICTIS*** Gaudry, 1861

Type species: Hyaenictis graeca Gaudry, 1861.

Other included species: Hyaenictis almerai Villalta Comella and Crusafont Pairó, 1948; *Hyaenictis hendeyi* Werdelin et al., 1994; ?*Hyaenictis wehaietu* Haile-Selassie and Howell, 2009.

Hyaenictis* aff. *almerai[1] Villalta Comella and Crusafont Pairó, 1948
(Figs. 2, 3 and 4a–c)

Holotype: MGB1605, partial right hemimandible from SMT (MN10, Spain).

Original description: "Relatively evolved *Hyaenictis*, having lost the p1, diastema very reduced; relatively robust mandible; shortened face, and canine in a more vertical position. m1 without metaconid. p2 long, slightly pointed and with a developed anterior cusp" (Villalta Comella and Crusafont Pairó 1948: 117, our translation from the Spanish original).

Tentatively referred material: IPS62078 from ROS-D, including: a partial cranium with left and right C1-M1; associated left and right hemimandibles with canines, left p3–m1, and right p2–m1 and m2; and associated atlas. See measurements in Table 1.

Description

Cranium The cranium preserves most of the palate, the snout and the left side of the neurocranium (including the zygomatic

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[1] For the use of open nomenclature we follow Bengtson (1988).

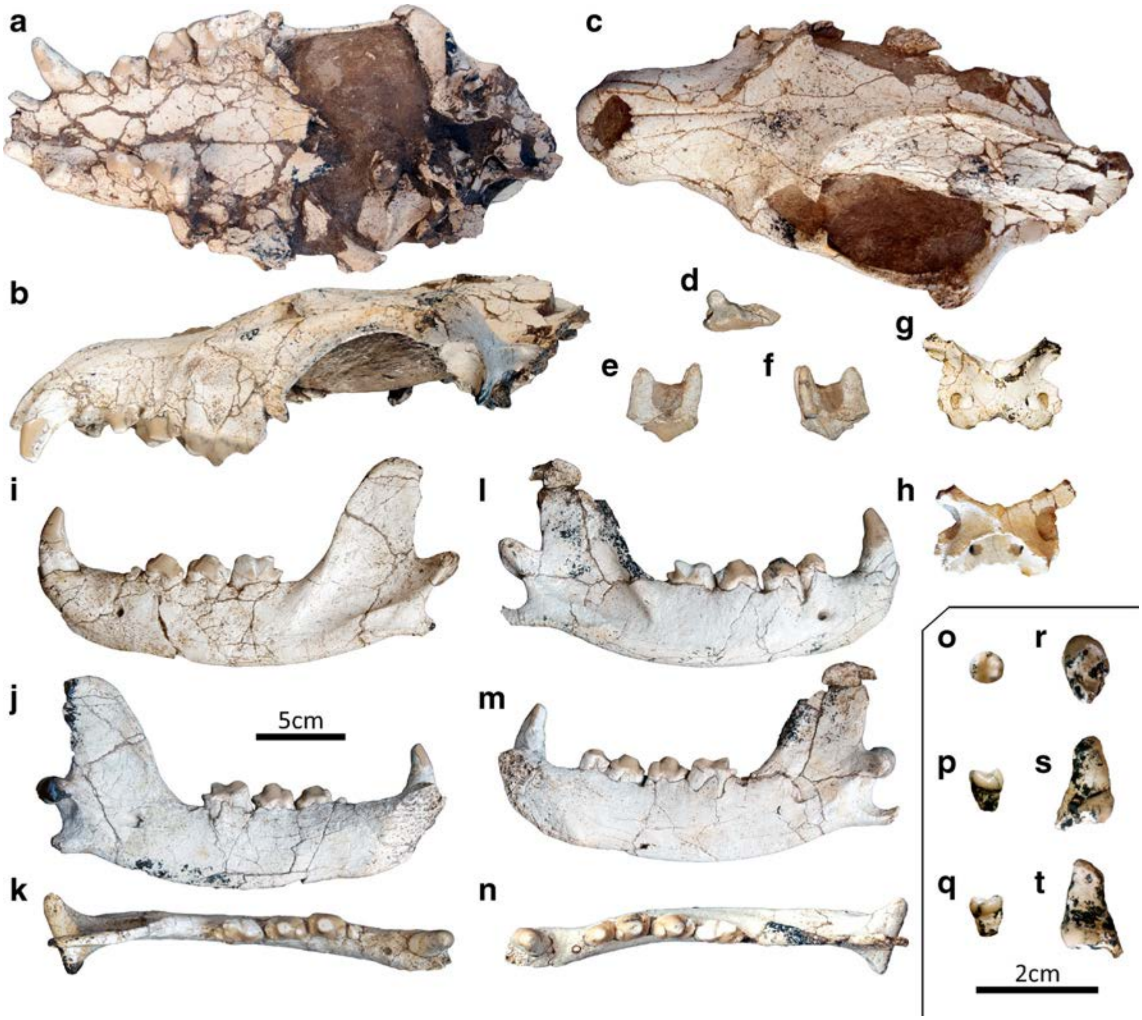

Fig. 2 *Hyaenictis* aff. *almerai* IPS62078 from ROS-D. **a–c**, cranium, in ventral (**a**), left lateral (**b**) and dorsal (**c**) views. **d–f**, right P4, in occlusal (**d**), labial (**e**) and lingual (**f**) views. **g–h**, atlas, in dorsal (**g**) and ventral (**h**) views. **i–k**, left hemimandible, in labial (**i**), lingual (**j**) and occlusal (**k**) views. **l–n**, right hemimandible, in labial (**l**), lingual (**m**) and occlusal (**n**) views. **o–q**, right m2 in occlusal (**o**), lingual (**p**) and labial (**q**) views. **r–t**, right M1 in occlusal (**r**), distal (**s**) and mesial (**t**) views. **o–t** are depicted at a different scale

arch), as well as the occipital condyles and the pterygoids (Fig. 2a–c). Most of the basicranium (basisphenoid and basioccipital) and the right side of the braincase (sphenoid complex, caudal end of the frontal, temporal, and parietal) are missing (Fig. 2a–c). The nasals are triangular, long and narrow, extending posteriorly nearly to the level of the postorbital processes (Fig. 2c). The infraorbital foramen is oval and in lateral view is located at the level of P3 (Fig. 2b). The zygomaticomaxillary suture is just above the P4, running from the anterior end of the orbit towards the distal root of P4 (Fig. 2b). The premaxillary-maxillary suture runs from the I3 root towards the mid-point of the nasals without reaching the frontal (Fig. 2c). The nasal aperture is wide and oval. The palate is wide at the level of P4 and narrows mesialwards to the canines (Fig. 2a). There is a slight postcanine constriction (Fig. 2c). The transverse palatine suture reaches the distal end of M1, as can be observed on the left side of the palate despite the presence of multiple cracks on this area (Fig. 2a). The palatine fissures are present at the level of the canine and are oval in shape (Fig. 2a). On the basicranium, the retroarticular processes are transversely wide and robust (Fig. 2a).

Mandible The two hemimandibles are almost complete, except for a small fragment of the right coronoid process and the distalmost part of the left angular process (Fig. 2i–n). The corpus is straight and slender, and has a single mental foramen below the p2 at about corpus midheight (Fig. 2i, l). The ramus is low, with a rounded coronoid process slightly expanded backwards and a condylar process that is located at about the same level as the occlusal plane (Fig. 2i, j, l, m). The masseteric fossa is deep and extends anteriorly until the level of m2 (Fig. 2i, l). The angular process is well developed and protrudes posteriorly beyond the condylar process (Fig. 2l, m).

Dentition The dentition is quite worn, with dentine exposure at the tips of the main and most of the accessory cusps. The

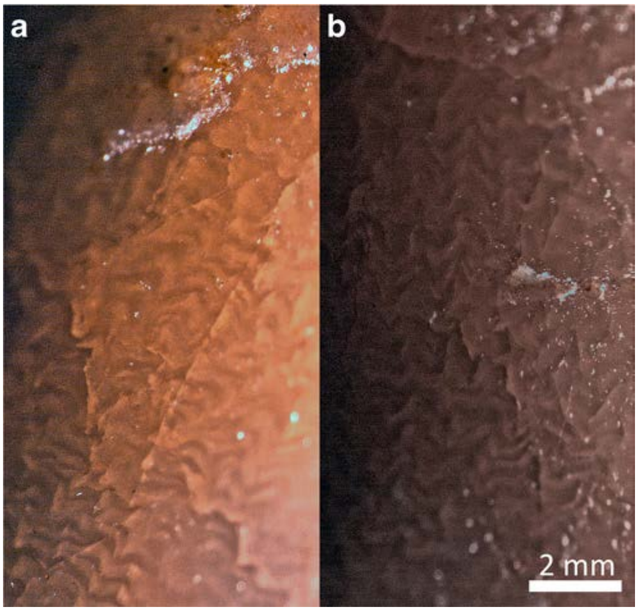

Fig. 3 Photographs of the HSB pattern on the outer enamel surface of the bottom crown portion of P3 (**a**) and the middle crown portion of p3 (**b**) in *Hyaenictis* aff. *almerai* IPS62078 from ROS-D. Apical is towards the top of the image. Note that the zig-zag HSB pattern of the middle crown portion progressively transforms into an acute-angled undulating HSB pattern (Tseng 2012) closer to the crown base of the P3 (**a**)

upper dentition is more complete on the left side, where the I3–M1 series is preserved, whereas on the right side the canine is broken, the P1 is missing, and the P4 and M1 are detached (Fig. 2a, d–f, r–t). The two I3s and the left canine are very worn. The P1 is buccolingually wider than mesiodistally long and displays a distal cingulum. The P2 has a blunt crest running from the protocone to the mesiolingual margin and a small distal accessory cusp just mesial to the distal cingulum. The P3 has two accessory cusps: the mesial one is rather small, located very close to the protocone and on the lingual half of the crown; the distal accessory cusp is broad but low, and located just mesial to the small cingulum present on the distal crown margin. The two P4s (Fig. 2a, d-f) are quite worn, so that only a few occlusal characters can be observed, including the presence of a well-developed protocone and of a parastyle that is mesiodistally shorter than the paracone. The M1 is present but similarly worn, and displays a subrectangular occlusal contour with no visible cusp features (Fig. 2a, r–t).

Most of the lower dentition is preserved, except for the incisors, the p1s, and the left p2 and m2 (Fig. 2i–q). The lower canines, like their upper counterparts, are quite worn. The diastema between the canine and p2 is moderately short and displays, closer to the p2, an alveolus for a single-rooted p1. All the remaining premolars are longer than wide but moderately stout, with a subrectangular (rather than oval) occlusal outline. The p2 has a small distal accessory cusp that is separated from the protoconid and from the distal cingulid by small notches. The p3 and p4 have better developed protoconids and two accessory cusps, the mesial one located towards the lingual side of the crown and the distal one situated on the marked distal cingulid (more buccally on p3 and more centrally on p4). The m1 paraconid and protoconid are too worn to observe their morphology, but it can be ascertained that the metaconid, located distolingually from

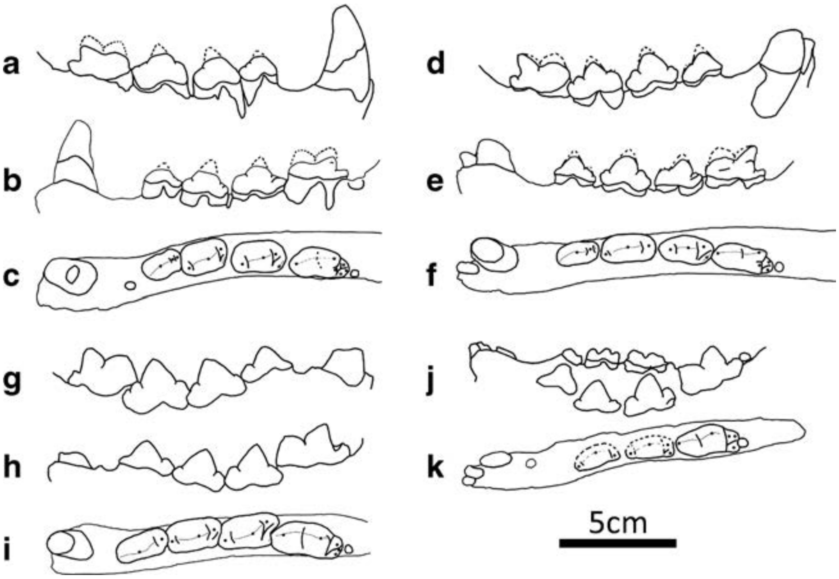

Fig. 4 Schematic drawings of the right postcanine toothrow of the ROS-D specimen and three species of *Hyaenictis*. **a–c**, *Hyaenictis* aff. *almerai* (IPS62070), in labial (**a**), lingual (**b**) and occlusal (**c**) views. **d–f**, *Hyaenictis hendeyi* (based on PQ-L21792 and the holotype PQ-L21000), in labial (**d**), lingual (**e**) and occlusal (**f**) views. **g–i**, *Hyaenictis almerai* (holotype, MGB16051), in labial (**g**), lingual (**h**) and occlusal (**i**) views. **j–k**, *Hyaenictis graeca* (holotype, MNHN-PIK-3002), in lingual (**j**) and occlusal (**k**) views. In the occlusal views, crests and cingulids are represented by *thin lines*, cuspids are denoted by *black dots*, and discontinuous lines represent inferred morphology (covered, missing and worn areas)

Table 1 Measurements (in mm) of *Hyaenictis* aff. *almerai* (IPS62078) from ROS-D. For measurement abbreviations, see the Materials and Methods

	PA	SKL	PB	SB	PS	FA	PN	PF	PST	LP1–P4	Woc	WiP4	WC	Hoc	
Skull	287.0	–	–	–	–	148.0	125.9	139.1	141.5	93.1	–	57.9	36.3	–	
	L C1	W C1	L P1	W P1	L P2	W P2	L P3	W P3	L P4	W P4	LP4pas	LP4pa	L P4m	L M1	W M1
Cranium (left)	18.8	5.8	8.9	7.0	19.7	11.1	25.7	14.2	37.2	20.5	–	–	–	6.2	10.3
Cranium (right)	–	–	–	–	20.3	11.9	26.0	15.4	37.8	20.9	–	–	–	6.7	10.4
	L c1	W c1	L p1	W p1	L p2	W p2	L p3	W p3	L p4	W p4	L m1	W m1	Ltm1	L m2	W m2
Mandible (left)	18.7	13.2	–	–	–	–	21.23	13.6	22.7	13.3	25.92	13.14	5.12	–	–
Mandible (right)	18.7	13.2	5.3	4.6	17.1	10.0	20.5	13.4	22.3	13.3	25.9	13.1	5.2	5.5	5.8

the protoconid, is only slightly developed and not completely isolated from the former cusp. The m1 talonid is much lower and shorter than the trigonid, and displays three main cuspids, of which the hypoconid is larger than the entoconid and hypoconulid. The m2 (Fig. 2o-q) has a round occlusal outline, a single trigonid cuspid (the mesially located paraconid), and two smaller talonid cuspids (entoconid and hypoconid) that are more distally situated.

With regard to tooth enamel microstructure, HSB are observable in all the lower and upper cheek teeth (at least on the bottom crown portion, and also, when preserved, in the middle of the crown wall, as the apical parts of the crowns are in all instances worn away). These bands clearly show a zig-zag pattern (Fig. 3) like that in extant bone-cracking hyaenids (Ferretti 1999; Tseng 2011, 2012) on the middle crown portions and, to some extent, on their bottom portion (although closer to the cervix the HSB pattern progressively becomes acute-angled undulating).

Atlas The atlas (Fig. 2g, h) is nearly complete, with only the wings broken. The vertebral arch is slender and medially displays a small craniodorsal protuberance. The lateral vertebral foramen and the transverse foramen are distinct (close to each other but not confluent), being anteriorly situated just below the alar notch, which is not very marked. The vertebral body is quite narrow and has a pointed protuberance on its caudal margin. The cranial articular fovea is wide and slightly expanded cranially on its dorsal portion.

Results

Morphological Comparisons with Other Miocene Hyaenids

Comparisons with Other Hyaenid Genera

Overall, the dentition of IPS62078 is more slender (it displays relatively narrower premolars) than *Adcrocuta eximia* (see Werdelin and Solounias 1990, 1991; Turner et al. 2008). IPS62078 further differs from *A. eximia* in the larger P4 protocone, the presence of a p3 mesial accessory cusp, the longer and tricuspid m1 talonid (instead of bicuspid, as *Adcrocuta* lacks the hypoconulid), and the retention of m2.

The dentition of the described specimen also does not resemble that of *Chasmaporthetes*, which is characterized by more slender and trenchant premolars with well-developed distal accessory cusps, as well as several more derived features that are absent in *Hyaenictis* spp. (Turner et al. 2008). Thus, IPS62078 differs from *Chasmaporthetes* (see Kurtén and Werdelin 1988; Werdelin and Solounias 1991; Werdelin and Turner 1996; Antón et al. 2006; Tseng et al. 2013) in the presence of p1, the relatively broader cheek teeth, the less developed accessory cusps in the premolars, the mesial and distal accessory cusps of the premolars aligned with the main cusp (instead of lingually tilted), the presence of metaconid (even if vestigial), the tricuspid m1 talonid (*Chasmaporthetes* lacks the hypoconulid and sometimes the hypoconid), and the presence of m2.

Compared to *Lycyaena*, the dentition of IPS62078 is larger, somewhat stouter (i.e., it displays relatively broader cheek teeth), and is further characterized by smaller and more indistinct premolar accessory cusps (Werdelin 1988; Werdelin and Solounias 1991). The specimen further differs from *Lycyaena* (see Werdelin 1988; Werdelin and Solounias 1991; Werdelin and Peigné 2010) in the occlusal morphology of the m1 (with a reduced instead of well-developed metaconid, and a shorter talonid with less developed cuspids), the presence of m2, and the deeper and stouter mandibular corpus.

In terms of mandibular robusticity and relative breadth of the lower premolars, IPS62078 resembles *Lycyaenops*, in spite of numerous differences in the occlusal morphology of the lower dentition (see Kretzoi 1938; Werdelin and Solounias 1991; Werdelin 1999; Werdelin and Peigné 2010). Thus, the described specimen mainly differs from *Lycyaenops* in the presence of p1, the better developed p3 accessory cusps, the less developed p4 distal accessory cusp, the presence of an m1 metaconid (even if reduced), and the longer and tricuspid (instead of bicuspid) m1 talonid.

With regard to tooth enamel microstructure, although the top portion of the cheek teeth crowns in IPS62078 are worn away, their preserved middle and bottom portions allow one to ascertain that, on the outer enamel surface, the HSB clearly display a zig-zag pattern (except closest to the cervix; Fig. 3). In this regard, the condition of the described specimen is most similar to *Chasmaporthetes*, in which the zig-zag pattern (unlike in extant and extinct fully-developed bone-cracking hyaenids, such as *Adcrocuta*) generally does not reach the base of the crown (Tseng 2012). In contrast, the condition of IPS62078 is much more similar to bone-cracking taxa than to that displayed by *Lycyaena*, which does not display a zig-zag pattern of HSB at any crown level (Tseng 2012).

Comparisons with Other Hyaenictis Species

The dentition of IPS62078 more closely resembles that of other species of *Hyaenictis*, except ?*H. wehaietu* from the late Miocene and early Pliocene of Ethiopia, which is smaller, lacks the p1 and m2, and further displays a well-developed and isolated m1 metaconid (Haile-Selassie and Howell 2009). In particular, IPS62078 resembles the other three species of *Hyaenictis* in the possession of a long and slender mandible with m2, the weak development of the mesial accessory cusp in the lower premolars, the short m1 without a well-developed metaconid, and the presence of more than a single cuspid in the m1 talonid (Werdelin et al. 1994).

Compared to the type species of the genus, *H. graeca* (Fig. 4j, k; Gaudry 1861; Howell and Petter 1985; Werdelin and Solounias 1990, 1991; Werdelin et al. 1994), IPS62078 (Fig. 4a–c) displays a similarly robust mandibular corpus that is only slightly curved on its inferior margin behind the m1 (although comparisons are hindered by the juvenile status of the holotype mandible of *H. graeca*). Both specimens also resemble one another in the retention of p1 and m2, as well as in the m1 occlusal morphology (characterized by a greatly reduced metaconid and a tricuspid talonid with a large hypoconid). However, IPS62078 differs from *H. graeca* in several features, namely the relatively broader lower premolars, the lower p2 protocone, the more restricted and simpler distal cingulids in the premolars, the p3 mesial accessory cusp, p3 aligned with the protoconid (instead of lingually tilted), and the smaller distal accessory cusp but larger distal crest in the p4.

IPS62078 differs even more clearly from *H. hendeyi* (Fig. 4d–f) from the earliest Pliocene of South Africa (Hendey 1974, 1978; Werdelin et al. 1994; Werdelin and Peigné 2010) in the relatively broader lower cheek teeth with a subrectangular (instead of elliptical) occlusal outline, the retention of the p1, the p2 with a lower protoconid and a smaller and more indistinct distal accessory cusp, and the tricuspid m1 talonid (instead of bicuspid, as *H. hendeyi* lacks the hypoconulid).

Differences are less marked when IPS62078 is compared with the holotype of *H. almerai* (Fig. 4g–i), from the similarly-aged Vallès-Penedès locality of SMT (Villalta Comella and Crusafont Pairó 1948; Werdelin and Solounias 1991; Werdelin et al. 1994), whose lower cheek teeth are somewhat more elongated (relatively narrower), but which nevertheless display a less oval occlusal outline than in *H. graeca* and *H. hendeyi* (thus more closely resembling IPS62078). Although the latter specimen resembles *H. almerai* (as well as *H. graeca* and *H. hendeyi*) in the retention of m2, it differs from *H. almerai* (and more closely resembles *H. graeca*) in the longer mandibular diastema and the presence of a p1 alveolus. Given the very small available sample sizes for European *Hyaenictis*, it cannot be discounted that the presence/absence of p1 was variable, as in some other hyaenids (e.g., *Lycyaena*; Werdelin 1988; Werdelin and Solounias 1991; Werdelin and Peigné 2010). In addition, in *H. hendeyi* the p1 is absent (Werdelin et al. 1994) suggesting that the presence of this tooth is variable in the genus as a whole. Nevertheless, IPS62078 further differs from *H. almerai* in several other occlusal features, including the smaller distal accessory cusp surrounded by a low distal cingulid in the p2, the mesial accessory cusps of the p3 and p4 aligned with the protoconid (instead of lingually tilted), and the more developed distal cingulid in the p4.

Morphometric Comparisons

Comparisons of dental size for the lower cheek teeth are reported by means of bivariate plots of buccolingual breadth (B) vs. mesiodistal length (L) in Fig. 5, whereas dental proportions are assessed by means of boxplots (Fig. 6) and ANOVA comparisons of log-transformed breadth/length index (BLI). Among the analyzed genera (*Adcrocuta*, *Chasmaporthetes*, *Lycyaena*, and *Hyaenictis* for p2–m1, and *Lycyaenops* for p2–p3), there are significant differences ($p < 0.001$) in dental proportions for all the analyzed lower cheek teeth ($F = 107.22$ for p2, $F = 79.16$ for p3, $F = 64.68$ for p4, and $F = 6.68$ for m1). Among other differences (see below), the bone-cracking *Adcrocuta* differs from the remaining genera (except for *Lycyaenops*) by displaying in all instances significantly broader premolars, with $p < 0.001$ (see also Figs. 5a–c and 6a–c). In the case of the lower carnassial, there are no significant differences between *Hyaenictis* and *Adcrocuta*, which tend to display a broader m1 than *Chasmaporthetes* and *Lycyaena* (although differences between *Hyaenictis* and *Chasmaporthetes* are not significant at $p < 0.05$; see also Figs. 5d and 6d). The lower carnassial is thus the least useful cheek tooth to discriminate between cursorial and bone-cracking hyaenids, and displays considerable overlap between all the analyzed genera. The proportions of the p2 (Fig. 6a) in *Hyaenictis* most closely resemble those of *Chasmaporthetes*, which are somewhat intermediate between the broader proportions of *Adcrocuta* and the narrower proportions ($p < 0.001$) of *Lycyaena*, although *Hyaenictis* does not significantly differ in this regard from any of the studied genera other than *Adcrocuta*. For both p3 (Figs. 5b and 6b) and p4

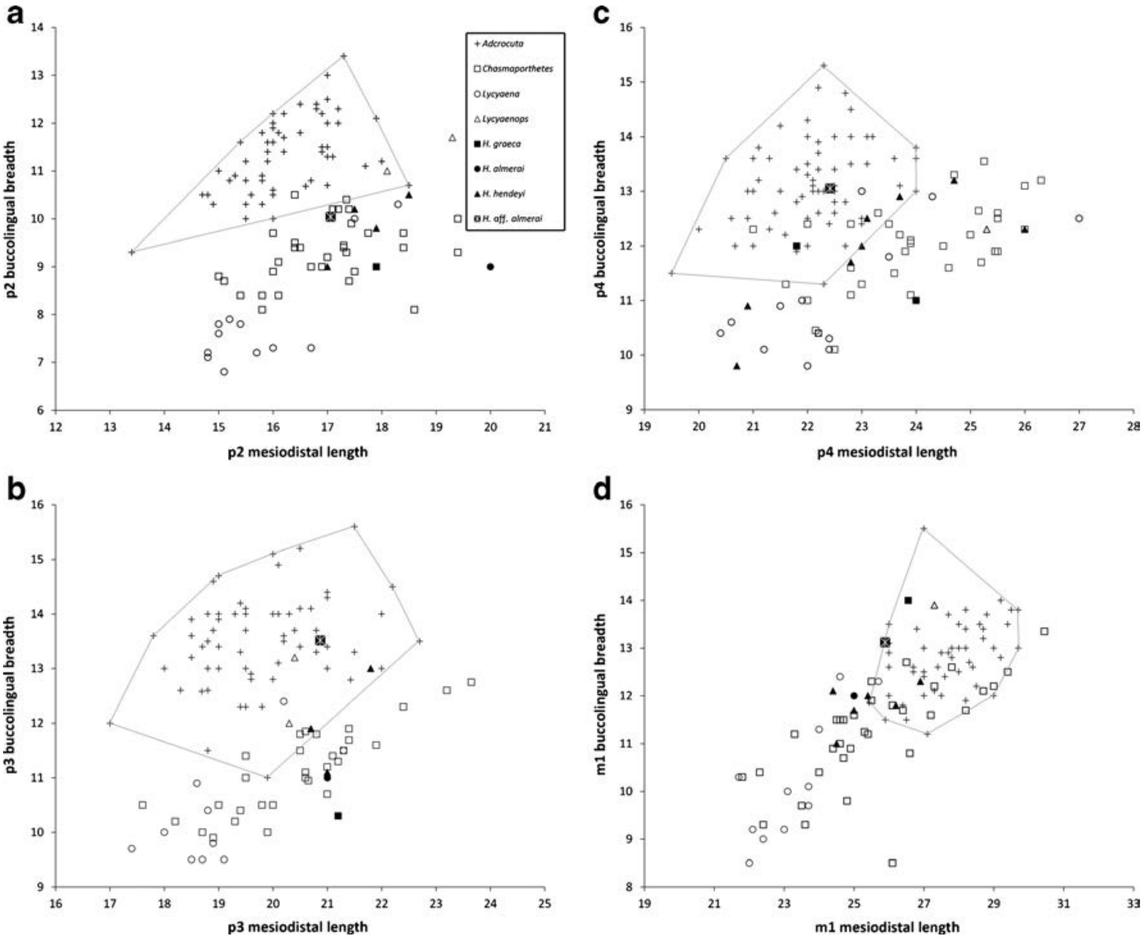

Fig. 5 Bivariate plots of buccolingual breadth vs. mesiodistal length in the cheek teeth of *Hyanictis* aff. *almerai*, compared with those of other selected Miocene hyaenids. **a**, p2. **b**, p3. **c**, p4. **d**, m1. Convex hulls encompass the range of variation in our sample of the bone-cracking *Acrocuta*

(Figs. 5c and 6c), all the cursorial hyaenids overlap and do not display significant differences among them, showing narrower proportions than *Adcrocuta* (although with some overlap, more marked in the p3 of *Lycyaenops*).

With regard to IPS62078, its p2 most closely resembles in both size (Fig. 5a) and proportions (Fig. 6a) those of *Chasmaporthetes* and *H. hendeyi*, thus being intermediate between *Lycyaena* and *Adcrocuta*. In contrast, for the remaining

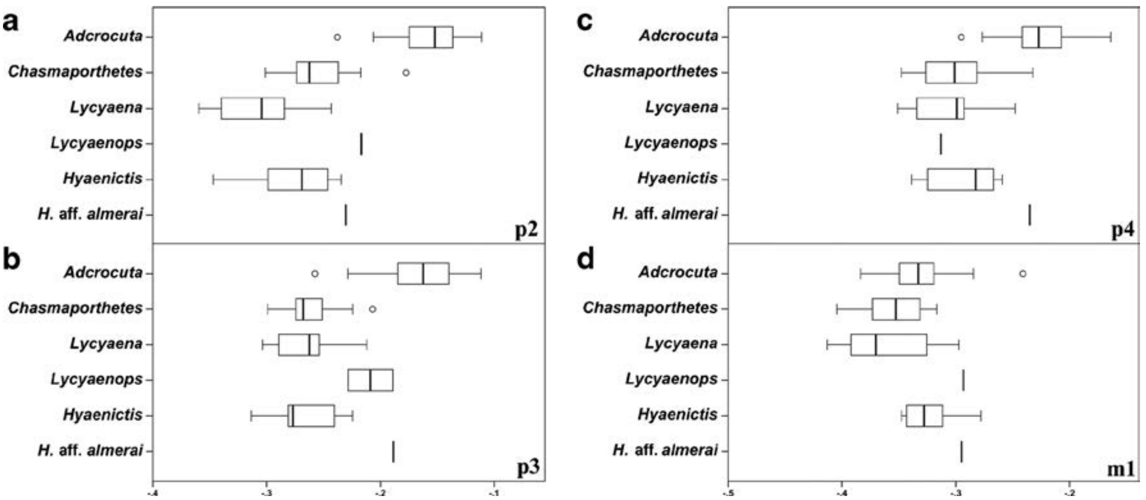

Fig. 6 Boxplots of breadth/length index (BLI) in the cheek teeth of *Hyaenictis* aff. *almerai*, compared with those of other selected Miocene hyaenids. **a**, p2. **b**, p3. **c**, p4. **d**, m1

premolars IPS62078 most clearly overlaps with *Adcrocuta* (Figs. 5b, c and 6b, c), generally displaying broader proportions than all the remaining analyzed hyaenids (including *Hyaenictis* spp.). Finally, for the m1 (Figs. 5d and 6d), IPS62078 most extensively overlaps with *Hyaenictis* and *Adcrocuta*, although as stated above all the studied genera overlap to a large extent. Overall, based on dental size and proportions, IPS62078 only most closely resembles species of *Hyaenictis* and other cursorial hyaenids regarding the p2 and the m1, whereas the p3 and p4 display a relative breadth closer to that of the bone-cracking *Adcrocuta*.

The PCA results (Fig. 7; Table 2) further confirm that the lower cheek tooth proportions of IPS62078 are intermediate between those of *Hyaenictis*, on the one hand, and those of *Adcrocuta*, on the other. A bivariate plot of PC2 vs. PC1 (Fig. 7) shows that *Adcrocuta* does not overlap with the cursorial hyaenids, and that IPS62078 falls close to (but outside) the convex hull depicting the variability of *Adcrocuta*, overlapping with the latter in the PC1 and with *Hyaenictis* (which more closely resembles *Chasmaporthetes* and *Lycyaena*) in the PC2. The investigated bone-cracking and cursorial hyaenids mostly differ in PC1, which explains most of the variance (85 %) and is largely driven by the buccolingual breadth of the premolars (mostly p2, but also p3 and p4). For this component, IPS62078 overlaps with *Adcrocuta* and falls far from the remaining *Hyaenictis* species and other cursorial hyaenids, as a result of the relatively broader p3 and p4 (which more closely resemble the condition of *Adcrocuta*). The PC2 explains 7 % of variance and is mostly positively driven by the breadth of the m1 and, to a lesser extent, the p4. On this axis, which segregates *Hyaenictis* spp. from both the cursorial hyaenids and *Adcrocuta* (with only minimal overlap), IPS62078 only overlaps with the former. Overall, the results of the PCA highlight that IPS62078 clearly differs from the analyzed cursorial hyaenids other than *Hyaenictis*, although it does not comfortably fit into the latter or *Adcrocuta*. Given that only three specimens of European *Hyaenictis* are available, it is not possible to confidently discount that their variability in dental proportions can be accommodated within a single genus. However, IPS62078 is clearly in this regard much more similar to (albeit less extreme than) the bone-cracking condition of *Adcrocuta*.

Table 2 Results of the principal component analysis based on breadth/length index (BLI) of the lower cheek teeth (p2 to m1) of *Hyaenictis* aff. *almerai* (IPS62078), compared with individuals of other selected Miocene hyaenid genera (*Hyaenictis*, *Adcrocuta*, *Chasmaporthetes*, and *Lycyaena*). For each principal component (PC), the loadings on each original variable are reported

	PC1	PC2	PC3	PC4
Eigenvalue	0.009281	0.000764	0.000520	0.000367
% variance	84.89	6.99	4.76	3.36
BLI p2 loading	0.651	−0.270	0.708	0.048
BLI p3 loading	0.598	−0.186	−0.649	0.432
BLI p4 loading	0.460	0.462	−0.197	−0.732
BLI m1 loading	0.090	0.824	0.196	0.524

Discussion

Taxonomic Attribution

The skull with mandible from ROS-D described in this paper (IPS62078) differs from the bone-cracking Miocene hyena *Adcrocuta* in several features, such as the presence of m2, the smaller premolar accessory cusps, the larger P4 protocone, the reduced m1 metaconid, and the tricuspid and longer m1 talonid. The former further differs from cursorial Miocene

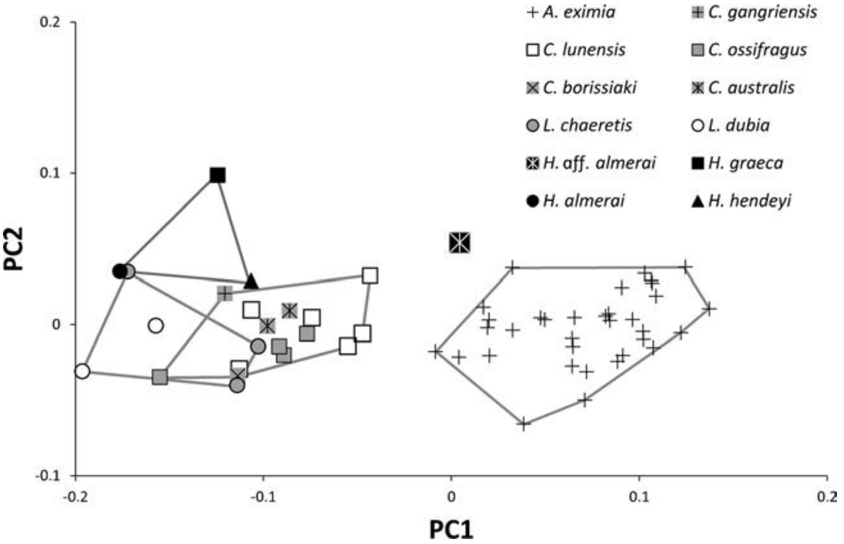

Fig. 7 Bivariate plot of the two first axes (PC2 vs. PC1) of the principal component analysis based on breadth/length index of the lower cheek teeth of *Hyaenictis* aff. *almerai*, compared with those of other selected Miocene hyaenids. The variability of each genus is denoted by convex hulls

hyenas, such as *Chasmaporthetes*, *Lycyaena*, and *Lycyaenops* in several occlusal features, namely: the presence of m2, the presence of p1 and the tricuspid m1 talonid (only compared to *Chasmaporthetes* and *Lycyaenops*), the shorter m1 talonid with smaller cuspids (compared to *Lycyaena*), the reduced m1 metaconid (instead of well developed, as in *Lycyaena*, or entirely absent, as in *Chasmaporthetes* and *Lycyaenops*), the smaller premolar accessory cusps (compared to *Chasmaporthetes* and *Lycyaena*, and to *Lycyaenops* in the case of the p4), and the lingually placed premolar accessory cusps (compared to *Chasmaporthetes*).

In the above-mentioned features and other characters, the described specimen from ROS-D (IPS62078) more closely resembles species of *Hyaenictis* other than ?*H. wehaietu*, and especially the Miocene European species *H. graeca* and *H. almerai*. Similarities include the presence of m2, the weakly developed anterior accessory cusps of the premolars, the P4 metastyle larger than the paracone, and the mesiodistally short m1 (with absent or greatly reduced metaconid, and a bicuspid or tricuspid talonid). In the retention of p1, IPS62078 more closely resembles *H. graeca*, although we do not consider this feature to be taxonomically relevant, as the small available samples preclude ascertaining whether this feature might have been variable in European *Hyaenictis*. In fact, the described specimen does not comfortably fit into any of these species, from which it differs in the stouter (relatively broader) lower premolars (especially p3 and p4), resulting in dental proportions that are intermediate between those of previously known *Hyaenictis* (plus other cursorial hyaenids such as *Chasmaporthetes*) and those of the bone-cracking *Adcrocuta*. IPS62078 further differs from other species of *Hyaenictis* (especially *H. graeca* and *H. hendeyi*) in some details of dental morphology, such as the more rectangular (less elliptical) occlusal outline of the premolars, the presence of a distal cingulid (behind the distal accessory cusp) in p2, and the lingually tilted mesial accessory cusps of the premolars (instead of aligned with the protoconid).

The above-mentioned differences preclude attribution of the described specimen to any of the previously known species of *Hyaenictis*. However, given that only a single individual is available from ROS-D and that the samples for both *H. graeca* and *H. almerai* are also very small, the possibility cannot be conclusively discounted that the above-mentioned differences in dental proportions and minor occlusal details merely reflect intraspecific variation. Specimen IPS62078 from ROS-D and the holotype of *H. almerai* have a similar geographic provenance and are roughly coeval (the former is no more than 0.5 million years younger, probably less). Taking all this evidence together, we choose to attribute IPS62078 to *Hyaenictis* aff. *almerai*. This assignment recognizes the closer morphological similarities with *H. almerai* and further takes into account the similar and age and geographic provenance, while at the same time it does not discount the possibility that IPS62078 represents a previously unknown species. Additional specimens from the late Miocene of the Vallès-Penedès Basin and elsewhere would be required to further ascertain the taxonomic allocation of European specimens currently attributed to *Hyaenictis* spp.

Implications for Feeding Behavior

European *Hyaenictis* have generally been included in the hyaenid ecomorphotype 4 (cursorial meat- and bone-eating hyenas, including among others *Chasmaporthetes* and *Lycyaena*), instead of ecomorphotype 5 (transitional bone-cracking hyenas, like *Belbus* Werdelin and Solounias, 1991, and *Metahyaena* Viranta and Werdelin, 2003) or 6 (fullydeveloped bone-cracking hyenas such as *Adcrocuta*; Werdelin 1996; Werdelin and Solounias 1996; Turner et al. 2008). However, some previous studies have favored some degree of durophagy in cursorial Miocene hyaenids such as *Chasmaporthetes*, in spite of noting their lesser bone-cracking abilities compared to fully developed bone-crackers (Kurtén and Werdelin 1988; Werdelin et al. 1994; Ferretti 1999; Antón et al. 2006). This was further confirmed by a finite elements analysis of the skull of *Chasmaporthetes* (Tseng et al. 2011), according to which this taxon would have been able to the resist the masticatory stresses generated by a bone-cracking diet (although less efficiently than *Crocuta*). In agreement with this, Tseng (2011, 2012) further showed that *Chasmaporthetes* displays a zig-zag pattern of HSB on the outer enamel surface of at least the top and middle crown portions of the premolars, and even on the bottom portion of p4, as is characteristic of all the cheek teeth of extant durophagous hyaenids and some extinct bone-cracking hyaenas (such as *Adcrocuta*, *Pliocrocuta* Kretzoi, 1938, and *Pachycrocuta* Kretzoi, 1938; Stefen 1997; Ferretti 1999, 2007; Stefen 1999; Stefen and Rensberger 1999; Tseng 2011, 2012; Vinuesa et al. 2014). While enamel microstructure is quite plastic from an evolutionary perspective (Tseng 2012), morphological changes in craniodental features most clearly evidence that some Miocene cursorial hyaenids such as *Chasmaporthetes* were, to some extent, already adapted to (albeit not specialized for) bone-cracking (Tseng et al. 2011). Based on the development of the zig-zag pattern of the HSB of IPS62078, *Hyaenictis* aff. *almerai* would have been at least as durophagous as *Chasmaporthetes*, although less so than *Adcrocuta*, which is entirely comparable to extant bone-cracking hyaenids and in some respects more derived than they are.

Furthermore, the premolar proportions of *Hyaenictis* aff. *almerai* from specimen IPS62078 (especially those of p3 and p4) are intermediate between those of *Chasmaporthetes* and previously known *Hyaenictis* spp., on the one hand, and those of *Adcrocuta*, on the other. This is shown not only by the breadth/length proportions of p3 and p4 separately, but also a multivariate analysis that takes into account all the lower cheek teeth (except p1) simultaneously. Our results therefore suggest for IPS62078 from ROS-D a higher commitment to durophagy than in other hyaenids customarily included in ecomorphotype 4 (including other *Hyaenictis*), thus being best qualified as a transitional bone-cracking hyena (ecomorphotype 5). This is further supported by other features of the described specimen, such as the deep masseteric fossa and the large insertions for the pterygoids, which are shown (although to a greater extent) by extant bone-cracking hyaenas as well as *Adcrocuta* (Werdelin and Solounias 1991, 1996; Turner et al. 2008). Unfortunately, the small available samples of European *Hyaenictis* preclude discerning whether IPS62078 differs from the latter in displaying greater durophagous adaptations (as it seems), or whether European *Hyaenictis* as a whole were somewhat intermediate between cursorial hyaenids such as *Chasmaporthetes* and fully-developed bone-crackers like *Adcrocuta*. In any case, the presence of some durophagous adaptations in the studied material, coupled with the fully-developed bone-cracking adaptations of the roughly coeval *Adcrocuta eximia* (which is first recorded in MN10 of Ravin de la Pluie, Greece; Bonis and Koufos 1981; Turner et al. 2008), support the contention that the early evolution of the bone-cracking ecomorphotype (the most common among extant hyaenids) in Europe was not related to competition with canids of the genus *Eucyon* Tedford and Qiu, 1996, which did not disperse from America into Eurasia until the Turolian (MN12; Sotnikova and Rook 2010).

Another interesting possibility raised by the present study derives from the fact that the earliest *Hyaenictis* (such as the one described here) and the earliest *Lycyaena* (i.e., *L. crusafonti*) are the most potentially durophagous species of their respective lineages (Kurtén 1976; Werdelin 1988; Werdelin and Solounias 1991; Werdelin et al. 1994). Therefore, it is possible that the earliest members of lineages within the *Chasmaporthetes* clade were more durophagous than later representatives of these lineages. This may imply that some degree of durophagy first evolved earlier than customarily assumed, in some (currently unknown) representative of the hyaenictitheres, and that reduction of durophagy subsequently evolved in parallel along several lineages.

Summary and Conclusions

Here, we describe a nearly complete skull with associated mandible and atlas of a medium-sized hyaenid from the late Miocene (MN10) of ROS-D (Vallès-Penedès Basin, NE Iberian Peninsula). Compared to other late Miocene hyaenids from Europe, the described specimen (IPS62078) most closely resembles the European species of *Hyaenictis* in several features, such as the retention of m2 and the reduced m1 metaconid. The described remains represent the most complete specimen recovered so far of European *Hyaenictis*, previously recorded from fragmentary remains attributed to *H. almerai* (MN10 of the same basin) and *H. graeca* (MN12 of Greece). In spite of the similar chronology and geographic provenance to *H. almerai*, IPS62078 from ROS-D is only tentatively assigned to this taxon (*Hyaenictis* aff. *almerai*). This is because the described specimen does not fit well into any of the previously known species of *Hyaenictis*, from which it differs by displaying cheek tooth proportions (in particular, relatively broader premolars) and other occlusal and mandibular features more similar to *Adcrocuta*, the earliest European hyaena with fully developed bone-cracking adaptations. Coupled with tooth enamel microstructure, this indicates a greater degree of durophagy in *H.* aff. *almerai* than previously recognized for *Hyaenictis*, seemingly intermediate between cursorial (ecomorphotype 4) and fully bone-cracking (ecomorphotype 6) hyaenids. This suggests that, during the Vallesian, bone-cracking adaptations evolved in parallel among several Eurasian hyaenid taxa due to selection pressures unrelated to competition with canids, which did not disperse from America into the Old Word until much later.

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References

Antón M, Turner A, Salesa M, Morales J (2006) A complete skull of *Chasmaporthetes lunensis* (Carnivora, Hyaenidae) from the Spanish Pliocene site of La Puebla de Valverde (Teruel). Estudios Geol 62: 375–388

Bataller JR (1921) Mamífers fòssils de Catalunya. Nota paleontològica. Butll Inst Cat Hist Nat 21: 80–86

Bengtson P (1988) Open nomenclature. Palaeontology 31: 223–227

Bonis L de, Koufos G (1981) A new hyaenid (Carnivora, Mammalia) in the Vallesian (late Miocene) of northern Greece. Sci Ann Fac Phys Math Univ Thessaloniki 21: 79–94

Cabrera L, Roca E, Garcés M, de Porta J (2004) Estratigrafía y evolución tectonosedimentaria oligocena superior-neógena del sector central del margen catalán (Cadena Costero-Catalana). In: Vera JA (ed) Geología de España. SGE-IGME, Madrid, pp 569–573

Casanovas-Vilar I, Alba DM, Robles JM, Moyà-Solà S (2011) Registro paleontológico continental del Mioceno de la cuenca del Vallès-Penedès. Paleontol Evol memòria especial 6: 55–80

Casanovas-Vilar I, Madern A, Alba DM, Cabrera L, García-Paredes I, van den Hoek Ostende L, DeMiguel D, Robles JM, Furió M, van Dam J, Garcés M, Angelone C, Moyà-Solà S (2015 published online) The Miocene mammal record of the Vallès-Penedès Basin (Catalonia). C R Palevol. doi:10.1016/j.crpv.2015.07.004

de Gibert JM, Casanovas-Vilar I (2011) Contexto geológico del Mioceno de la cuenca del Vallès-Penedès. Paleontol Evol memòria especial 6: 39–45

Evans HE, de Lahunta A (2013) Miller's Anatomy of the Dog. 4th ed. Elsevier, St. Louis

Ferretti MP (1999) Tooth enamel structure in the hyaenid *Chasmaporthetes lunensis lunensis* from the late Pliocene of Italy, with implications for feeding behavior. J Vertebr Paleontol 19: 767–770

Ferretti MP (2007) Evolution of bone-cracking adaptations in hyaenids (Mammalia, Carnivora). Swiss J Geosci 100: 108–128

Gaudry A (1861) Note sur les carnassiers fossiles de Pikermi (Grèce). Bull Soc Geol Fr 18: 527–538

Ginsburg L (1977) Les carnivores du Miocène de Beni Mellal (Maroc). Geol Mediterr 4: 225–240

Haile-Selassie Y, Howell FC (2009) Carnivora. In: Haile-Selassie Y, WoldeGabriel G (eds) *Ardipithecus kadabba:* Late Miocene Evidence from the Middle Awash, Ethiopia. University of California Press, Berkeley, pp 237–275

Hammer Ø, Harper DAT (2006) Paleontological Data Analysis. Blackwell Publishing, Malden

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontol Electron 4(1): Art. 4 [9 pp.]. http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Hendey QB (1974) The late Cenozoic Carnivora of the south-western Cape Province. Ann S Afr Mus 63: 1–369

Hendey QB (1976) The Pliocene fossil occurrences in 'E' Quarry, Langebaanweg, South Africa. Ann S Afr Mus 69: 215–247

Hendey QB (1978) Late Tertiary Hyaenidae from Langebaanweg, South Africa, and their relevance to the phylogeny of the family. Ann S Afr Mus 76: 265–297

Howell FC, Petter G (1985) Comparative observations on some middle and upper Miocene hyaenids. Genera: *Percrocuta* Kretzoi, *Allohyaena* Kretzoi, *Adcrocuta* Kretzoi (Mammalia, Carnivora, Hyaenidae). Geobios 18: 419–476

Koufos GD (2011) The Miocene carnivore assemblage of Greece. Estudios Geol 67: 291–320

Kretzoi M (1938) Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtfauna. Ann Mus Nat Hung 31: 88–157

Kurtén B (1976) Fossil Carnivora from the late Tertiary of Bled Douarah and Cherichira, Tunisia. Notes Serv géol Tunis 42: 177–214

Kurtén B, Werdelin L (1988) A review of the genus *Chasmaporthetes* Hay, 1921 (Carnivora, Hyaenidae). J Vertebr Paleontol 8: 46–66

Madurell-Malapeira J, Robles JM, Casanovas-Vilar I, Abella J, Obradó P, Alba DM (2014) The scimitar-toothed cat *Machairodus aphanistus* (Carnivora: Felidae) in the Vallès-Penedes Basin (NE Iberian Peninsula). C R Palevol 13: 569–585

Morales J, Pickford M, Soria D (2005) Carnivores from the late Miocene and basal Pliocene of the Tugen Hills, Kenya. Rev Soc Geol Esp 18: 39–61

Qiu Z (1987) Die Hyaeniden aus dem Ruscinium und Villafranchium Chinas. Münch Geowiss Abh A 9: 1–108

Solounias N (1981) The Turolian fauna from the island of Samos, Greece, with special emphasis on the hyaenids and the bovids. Contrib Vertebr Evol 6: 1–232

Sotnikova M, Rook L (2010) Dispersal of the Canini (Mammalia, Canidae: Caninae) across Eurasia during the late Miocene to early Pleistocene. Quaternary Internatl 212: 86–97

Stefen C (1997) Differentiations in Hunter-Schreger bands of carnivores. In: Koenigswald Wv, Sander PM (eds) Tooth Enamel Microstructure. A.A. Balkema, Rotterdam, pp 123–136

Stefen C (1999) Enamel microstructure of recent and fossil Canidae (Carnivora: Mammalia). J Vertebr Paleontol 19: 576–587

Stefen C, Rensberger JM (1999) The specialized structure of hyaenid enamel: description and development within the lineage—including percrocutids. Scanning Microsc 13: 363–380

Tseng ZJ (2011) Variation and implications of intra-dentition Hunter-Schreger band pattern in fossil hyaenids and canids (Carnivora, Mammalia). J Vertebr Paleontol 31: 1163–1167

Tseng ZJ (2012) Connecting Hunter-Shreger band microstructure to enamel microwear features: new insights from durophagous carnivores. Acta Palaeontol Pol 57: 473–484

Tseng ZJ, Antón M, Salesa MJ (2011) The evolution of the bone-cracking model in carnivorans: cranial functional morphology of the Plio-Pleistocene cursorial hyaenid *Chasmaporthetes lunensis* (Mammalia, Carnivora). Paleobiology 37: 140–156

Tseng ZJ, Li Q, Wang X (2013) A new cursorial hyaena from Tibet, and analysis of biostratigraphy, paleozoogeography, and dental morphology of *Chasmaporthetes* (Mammalia, Carnivora). J Vertebr Paleontol 33: 1457–1471

Turner A (1988) On the claimed occurrence of the hyaenid genus *Hyaenictis* Gaudry at Swartkrans (Mammalia, Carnivora). Ann Transvaal Mus 34: 523–533

Turner A, Antón M, Werdelin L (2008) Taxonomy and evolutionary patterns in the fossil Hyaenidae of Europe. Geobios 41: 677–687

Villalta Comella JF de, Crusafont Pairó M (1941) Noticia preliminar sobre la fauna de carnívoros del Mioceno continental del Vallés-Penedés. Bol R Soc Esp Hist Nat 39: 201–208

Villalta Comella JF de, Crusafont Pairó M (1943) Los vertebrados del Mioceno continental de la cuenca del Vallés-Panadés (provincia de Barcelona). I. Insectívoros. II. Carnívoros. Bol Inst Geol Min Esp 56: 145–336

Villalta Comella JF de, Crusafont Pairó M (1948) Nuevas aportaciones al conocimiento de los carnívoros pontienses del Vallés-Penedés. In: Miscelánea Almera. Publ Inst Geol 7: 81–121

Vinuesa V, Madurell-Malapeira J, Ansón M, Alba DM (2014) New cranial remains of *Pliocrocuta perrieri* (Carnivora, Hyaenidae) from the Villafranchian of the Iberian Peninsula. Boll Soc Paleontol Ital 53: 39–47

Werdelin L (1988) Studes of fossil hyaenas: the genera *Thalassictis* Gervais ex Nordmann, *Palhyaena* Gervais, *Hyaenictitherium* Kretzoi, *Lycyaena* Hensel and *Palinhyaena* Qiu, Huang & Guo. Zool J Linn Soc 92: 211–265

Werdelin L (1996) Community-wide character displacement in Miocene hyaenas. Lethaia 29: 97–106

Werdelin L (1999) Studies of fossil hyaenas: affinities of *Lycyaenops rhomboideae* Kretzoi from Pestlörinc, Hungary. Zool J Linn Soc 126: 307–317

Werdelin L, Peigné WJ (2010) Carnivora. In: Werdelin L, Sanders WJ (eds) Cenozoic Mammals of Africa. University of California Press, Berkeley, pp 603–657

Werdelin L, Solounias N (1990) Studies of fossil hyaenids: the genus *Adcrocuta* Kretzoi and the interrelationships of some hyaenid taxa. Zool J Linn Soc 98: 363–386

Werdelin L, Solounias N (1991) The Hyaenidae: taxonomy, systematics and evolution. Fossils Strata 30: 1–104

Werdelin L, Solounias N (1996) The evolutionary history of hyaenas in Europe and western Asia during the Miocene. In: Bernor RL, Fahlbusch V, Mittmann H-W (eds) The Evolution of Western Eurasian Neogene Mammal Faunas. Columbia University Press, New York, pp 290–306

Werdelin L, Turner A (1996) The fossil Hyaenidae of Africa: present status. In: Stewart KM, Seymour KL (eds) Palaeoecology and Palaeoenvironments of Late Cenozoic Mammals. University of Toronto Press, Toronto, pp 637–659

Werdelin L, Turner A, Solounias N (1994) Studies of fossil hyaenids: the genera *Hyaenictis* Gaudry and *Chasmaporthetes* Hay, with a reconsideration of the Hyaenidae of Langebaanweg, South Africa. Zool J Linn Soc 111: 197–217

Chapter 5. New cranial remains of *Pliocrocuta perrieri* (Carnivora, Hyaenidae) from the Villafranchian of the Iberian Peninsula

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Summary: This work describes three previously unpublished skulls of *Pliocrocuta perrieri* from Villarroya and La Puebla de Valverde. The skulls are compared to the closest relatives of this taxon, *Chasmaporthetes lunensis* and *Pachycrocuta brevirostris*.

Author's contribution: The doctoral candidate is the first author and was involved in all the stages of the study, including the description of the specimens, the statistical analyses and the writing of the manuscript.

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New cranial remains of *Pliocrocuta perrieri* (Carnivora, Hyaenidae) from the Villafranchian of the Iberian Peninsula

Víctor Vinuesa, Joan Madurell-Malapeira, Marco Ansón & David M. Alba

V. Vinuesa, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Campus de la UAB s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain; victor.vinuesa@icp.cat

J. Madurell-Malapeira, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Campus de la UAB s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain; Dipartimento di Scienze della Terra, Università di Roma "La Sapienza", P.le A. Moro 5, I-00185 Roma, Italy; joan.madurell@icp.cat; corresponding author

M. Ansón, Departamento de Dibujo, Facultad de Bellas Artes, Universidad Complutense de Madrid, c/ Greco 2, 28040 Madrid; Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, c/ José Antonio Nováis 2, 28040 Madrid, Spain; paleomarco@yahoo.es

D.M. Alba, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Campus de la UAB s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain; Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy; david.alba@icp.cat

KEY WORDS - Hyaenidae, Pliocrocuta*, Villarroya, La Puebla de Valverde, Villafranchian, Plio-Pleistocene.*

ABSTRACT - The hyaenid Pliocrocuta perrieri *is one of the commonest large carnivoran species in the European Late Pliocene and Early Pleistocene, being recorded from more than 20 sites across the Old World. In spite of this, adult and fairly complete crania of this species have been only recovered from the French locality of Saint-Vallier (Early Pleistocene, MN17). Here we describe three new crania of this bone-cracking hyena from the classic Iberian localities of Villarroya (Late Pliocene, MN16a) and La Puebla de Valverde (Early Pleistocene, MN17). The morphology of the new crania is compared (both qualitatively and metrically) with that of previously known craniodental remains of* P. perrieri*, as well as with that of other extinct hyaenids, including its closest relative (*Pachycrocuta brevirostris*) and the contemporaneous* Chasmaporthetes lunensis*. The described skulls display many morphological and morphometric similarities with previously-known specimens of* P. perrieri*, including the relatively long muzzle, the triangular, slender and long nasals, the relatively short P2, and other occlusal details. In contrast, the new specimens display significant differences compared with both* C. lunensis *(the shorter muzzle, the more anterior orbits and more posterior infraorbital foramen, the triangular nasals, and the broader premolars with a relatively shorter P2) and* Pa. brevirostris *(smaller craniodental size, longer muzzle, and various dental occlusal details). The new skulls of* P. perrieri *reported here enable a more complete evaluation of intraspecific variability in this taxon, and the study of their internal anatomy might provide, in the future, new data on the paleoecology of* P. perrieri *and its phylogenetic relationships with other bone-cracking hyenas, both extant and extinct.*

RIASSUNTO - [Nuovi resti cranici di *Pliocrocuta perrieri* (Carnivora, Hyaenidae) dal Villafranchiano della Penisola Iberica] - *Lo ienide* Pliocrocuta perrieri *è una delle specie di grandi carnivori più comuni nel Pliocene Superiore e Pleistocene Inferiore d'Europa, registrata in più di 20 siti in tutto il Vecchio Mondo. Tuttavia, crani adulti e abbastanza completi di questa specie sono noti solo nella località francese di Sant-Vallier (Pleistocene Inferiore, MN17). In questa nota vengono descritti tre nuovi crani di questa iena frantumatrice di ossa provenienti dalle note località della Penisola Iberica di Villarroya (Pliocene Superiore, MN16a) e La Puebla de Valverde (Pleistocene Inferiore, MN17). La morfologia dei nuovi crani viene confrontata (qualitativamente e metricamente) con quella dei resti craniodentari già conosciuti di* P. perrieri*, nonché con quella di altri ienidi estinti, incluso il suo parente più vicino (*Pachycrocuta brevirostris*) e la specie coeva* Chasmaporthetes lunensis*. I crani descritti mostrano molte somiglianze morfologiche con gli esemplari già noti di* P. perrieri*, tra cui il muso relativamente allungato, i nasali triangolari, snelli e lunghi, il P2 relativamente corto, ed altri dettagli della morfologia occlusale. Al contrario, i nuovi esemplari mostrano differenze importanti rispetto a* C. lunensis *(il muso più corto, le orbite posizionate anteriormente e il foramen infraorbitale più posteriore, i nasali triangolari, e i premolari superiori più larghi, con il P2 relativamente più corto) e* Pa. brevirostris *(dimensioni craniodentali più piccole, muso più lungo, presenza di cuspidi accessorie mesiali in P2 e P3, ed altri dettagli della morfologia occlusale dei denti). L'attribuzione tassonomica degli esemplari descritti a* P. perrieri *è ulteriormente confermata dai risultati dell'analisi multivariata basata su dimensioni e proporzioni dei premolari superiori. I nuovi crani di* P. perrieri *rappresentano una aggiunta significativa alla conoscenza di questa specie di ienide, poiché permettono una valutazione più completa della variabilità interspecifica nelle caratteristiche craniodentali. Peraltro, lo studio dell'anatomia cranica interna negli esemplari descritti potrebbe fornire, in futuro, nuovi data sulla paleoecologia di* P. perrieri *e sulle sue relazioni filogenetiche con le altre iene frantumatrici di ossa, sia attuali sia estinte.*

INTRODUCTION

The bone-cracking hyena *Pliocrocuta perrieri* (Croizet & Jobert, 1828) (Carnivora, Hyaenidae) is one of the large carnivorans most commonly recorded in the Early to Middle Villafranchian of Eurasia, being also frequently associated with the hunting hyena *Chasmaporthetes lunensis* (Del Campana, 1914). The chronological range of *P. perrieri* spans from MN15 to MN17 (4.2-2.0 Ma; Turner et al., 2008), whereas geographically it is widely distributed across Eurasia and Africa (Werdelin & Solounias, 1991; Turner et al., 2008). Until recently, it was generally considered that this species went locally extinct in Europe by the end of the Middle Villafranchian, so that its purported Middle Pleistocene record was interpreted as a second dispersal event from Africa (Turner et al., 2008). It is currently recognized, however, that its presumed second dispersal event corresponds in fact to that of another taxon, *Hyaena prisca* De Serres, Dubreuil & Jeanjean, 1828 (see Madurell-Malapeira, 2010). From a phylogenetic viewpoint, *Pliocrocuta* is considered the sister-taxon of *Pachycrocuta* Kretzoi, 1938 (Werdelin & Solounias, 1991;

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Turner et al., 2008), or even its direct ancestor (Howell & Petter, 1980; Werdelin & Solounias, 1991; Arribas & Palmqvist, 1999; Olive, 2006; Turner et al., 2008).

Pliocrocuta perrieri is a large-bodied hyaenid dentally characterized by a non-reduced P4 protocone, as well as a short and massive m1 with no metaconid but with a wide talonid, in which both the entoconid and hypoconid are present (Werdelin & Sanders, 2010). Since its original description as *Hyaena perrieri* Croizet & Jobert, 1828, the taxonomic status of this taxon has been subject to considerable controversy (Turner, 1990; Werdelin & Solounias, 1991). Kretzoi (1938) erected the genus *Pliocrocuta*, which was subsequently synonymized with *Pachycrocuta* by several authors (Ficcarelli & Torre, 1970; Howell & Petter, 1980). More recently, Turner (1990) and Werdelin & Solounias (1991) resurrected the genus *Pliocrocuta* and further noted that *Pliocrocuta pyrenaica* (Depéret, 1890) and *Hyaena arvernensis* (Croizet & Jobert, 1828) must be considered junior subjective synonyms of *P. perrieri.*

In spite of being a relatively common taxon, *P. perrieri* is mostly known from dentognathic or isolated dental specimens. Thus, its postcranial anatomy is virtually unknown, and fairly complete crania have been only reported from the localities of Saint-Vallier (MN17, France) and Zhangwagou (MN15, China) (Viret, 1954; Qiu, 1987). Here we describe three fairly complete unpublished crania and associated mandibular remains of *Pliocrocuta perrieri* from the Iberian localities of Villarroya (MN16a) and La Puebla the Valverde (MN17), which provide new data on the intraspecific variability of the craniodental morphology of this taxon, and enable us to further review the differences of *Pliocrocuta* compared to other hyaenids.

MATERIALS AND METHODS

Abbreviations

ICP - Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona (Spain). IPS - Acronym of the collections of the ICP. MNHN - Muséum National d'Histoire Naturelle, Paris (France).

Comparative material

We compared the described material with the two other known adult complete crania of *P. perrieri* (QSV20 and QSV48), from the French locality Saint Vallier (Viret, 1954; Howell & Petter, 1980; Werdelin & Solounias, 1991). The other available crania of this species (V7283, V7284), from the Chinese locality of Zhangwagou (Qiu, 1987), were not taken into account in the comparisons due to their juvenile condition. Dental measurements (in mm) for *P. perrieri*, *C. lunensis* and *Pachycrocuta brevirostris* (Gervais, 1850) (regarding the autorship of the taxon, see Alba et al., in press) were taken from the literature (Viret, 1954; Adrover & Soria, 1976; Howell & Petter, 1980; Qiu, 1987; Geraads, 1997; Turner, 2001; Argant, 2004; Baryshnikov & Tsoukala, 2010; Werdelin & Lewis, 2012). When the two dental rows were available for a single individual, the averages of right and left measurements were used. Dental enamel microstructure in the described specimens was evaluated using light microscope, in order to identify the type of Hunter-Shreger bands (HSB; Koenigswald & Sander, 1997; Ferretti, 1999) displayed by them.

Morphometric comparisons

Craniodental measurements of the described specimens were taken to the nearest 0.01 mm with a digital caliper. Dental size and proportions were assessed using bivariate plots of buccolingual width vs. mesiodistal length for the P2, P3 and P4, as well as a plot of P2 length vs. that of the whole upper premolar series (P2-P4). With regard to multivariate comparisons, a canonical variate Discriminant Analysis (DA) was performed with SPSS v. 20.0, based on the mesiodistal lengths and buccolingual widths for the P2, P3 and P4. Three groups were defined a priori (*P. perrieri*, *C. lunensis* and *Pa. brevirostris*), and two of the described crania were left ungrouped, being classified a posteriori by the analysis. Only IPS36758 and IPS36759 were included in the analysis, due to the impossibility of measuring tooth widths in IPS27340.

GEOLOGICAL BACKGROUND

Villarroya

The site of Villarroya is located in the Villarroya lacustrine Basin (Northern Iberian Peninsula; Fig. 1; Anadón et al., 2009). It is a classic paleontological site from the Early Villafranchian of Europe (Carvajal, 1926; Villalta Comella, 1952; Arribas Herrera & Bernad García, 1994; Jiménez García et al., 1999), from which more than twenty macromammalian species have been identified (Jiménez García et al., 1999). The age of Villarroya is currently correlated to MN16a (Arribas Herrera & Bernad García, 1994; Jiménez García et al., 1999), with an estimated age of ca. 2.6 Ma (Agustí & Oms, 2001).

La Puebla de Valverde

La Puebla de Valverde is located in the Sarrión plateau within the Teruel basin (Eastern Iberian Peninsula; Fig. 1; Gautier & Heintz, 1974). Like Villarroya, it is considered one of the most relevant mammal sites of

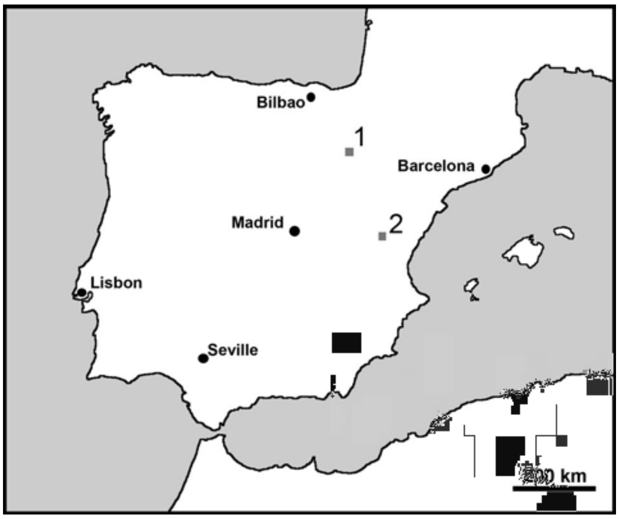

Fig. 1 - Location map of the studied sites within the Iberian Peninsula. 1: Villarroya; 2: La Puebla de Valverde.

the Middle Villafranchian of Europe (Crusafont Pairó et al., 1964; Adrover et al., 1974; Gautier & Heintz, 1974; Alcalá, 1994; Alberdi et al., 1997), with 21 identified macromammal species (Alberdi et al., 1997). The site is currently correlated to MN17 (Alcalá, 1994; Alberdi et al., 1997), with an estimated age of 2.14-1.95 Ma (Sinusía et al., 2004).

SYSTEMATIC PALEONTOLOGY

Order Carnivora Bowdich, 1821
Family Hyaenidae Gray, 1821
Subfamily Hyaeninae Gray, 1821

Genus *Pliocrocuta* Kretzoi, 1938

Type species - *Hyaena perrieri* Croizet & Jobert, 1828

Pliocrocuta perrieri (Croizet & Jobert, 1828)
(Figs 2-3)

Holotype - MNHN coll. Croizet No. 834, mandible from Les Étouaires (MN17, France).

Referred specimens - Cranium from Villarroya (IPS36758; Figs 2a, 3a); skull from Villarroya (IPS36759; Figs 2b, 3b); skull from La Puebla de Valverde (IPS27340; Fig. 2c).

Description and comparisons

Preservation - The cranium IPS36758 (Fig. 2a) is not completely preserved, missing the zygomatic arches, the tympanic bullae, and the posterior end of the sagittal crest. The specimen is also slightly distorted along its length, and displays abundant minor fractures, which are located along the braincase, the frontal and the nasals. The dentition (Fig. 3a) is heavily worn, but generally well preserved, although the left P2 is partially broken, and the canines and several incisors (right I1 and I2) are missing. The left I2 is preserved but incorrectly glued to the premaxilla (it is rotated and the apex-root axis is inverted). Part of the left mandibular corpus (with p2-p3 and the mesial portion of p4) is preserved, being attached to the cranium above the right maxilla.

The cranium IPS36759 (Fig. 2b) is undistorted and completely preserved, except for the two tympanic bullae and the zygomatic arches, which are missing. The morphology is generally well preserved, in spite of displaying a vertical fracture at about skull mid-length (just behind the orbits), which is oriented roughly along the coronal plane. There are several additional minor fractures, especially around the tooth rows, which are filled with plaster. The dentition (Fig. 3b) is very worn; only the two P1 are missing, although the left I1, P4, M1 and the right I1 and P4 are only partially preserved.

Unlike the two other specimens, IPS27340 (Fig. 2c) displays the mandible attached to the cranium in anatomical position. The cranium is more distorted, and displays a major fracture between the neurocranium and the nasals. Moreover, the posterior portion of the skull is slightly rotated and anteriorly displaced (overlapping with the nasals). The left side of the braincase is covered with sediment that was not removed during the preparation (due to the fragility of the specimen), so that only a portion of the sagittal crest is visible. The right side of the neurocranium is partially broken at the parietal and basicranial areas, exposing a large portion of the brain endocast and the tympanic bulla. In the anterior portion of the cranium, the left maxilla is almost complete, and part of the left zygomatic arch and orbit are also preserved, further displaying a fracture between P3 and P4. The infraorbital foramina, the nasals and the nasal fossa are missing. The right maxilla is poorly preserved, only

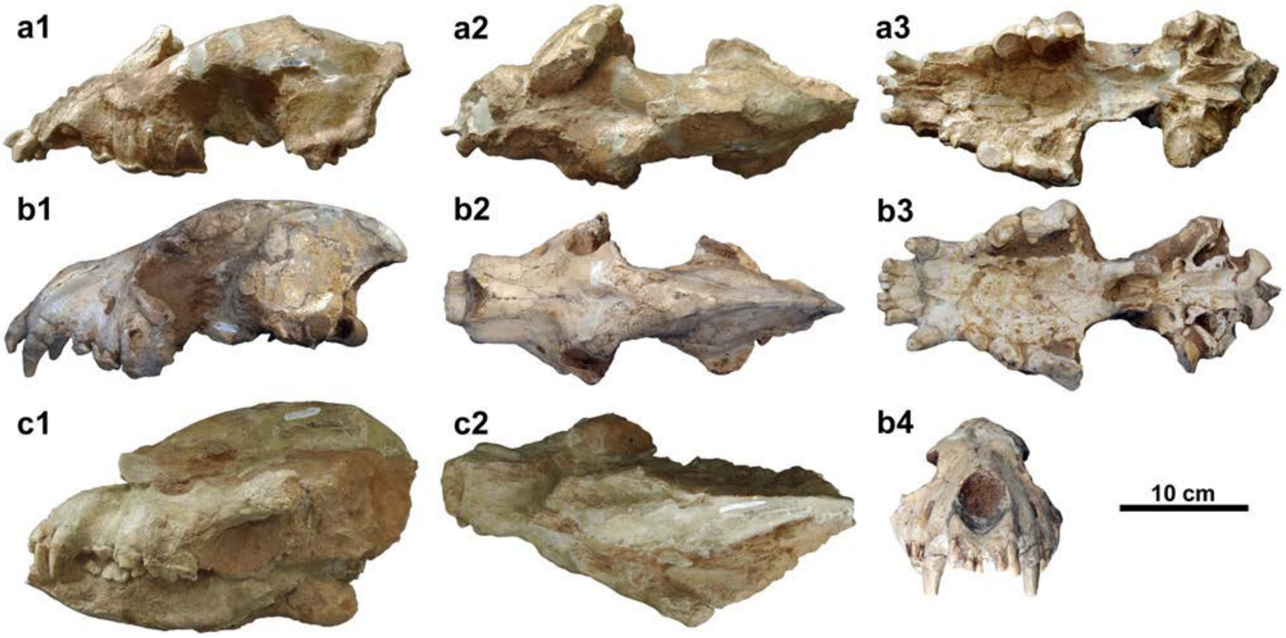

Fig. 2 - Skulls of *Pliocrocuta perrieri* from Villarroya and La Puebla de Valverde. IPS36758: a1) left lateral view, a2) dorsal view, a3) basal view; IPS36759: b1) left lateral view, b2) dorsal view, b3) basal view, b4) frontal view; IPS27340: c1) left lateral view, c2) dorsal view.

Specimen	Side	PA	SKL	PB	SB	PS	FA	PN	PF	PT	LP1-P4	Woc	WP4	WC	Hoc
IPS36759	—	285.0	250.0	237.0	65.7	172.9	160.0	112.2	142.9	138.1	81.2	54.1	97.5	40.2	94.3
IPS36758	—	255.0	—	218.0	74.0	155.0	138.0	129.0	126.1	130.3	81.0	—	90.8	40.5	77.0
IPS27340	—	—	—	—	—	—	—	—	—	—	88.9	—	—	—	—
Specimen	**Side**	**LC1**	**WC1**	**LP1**	**WP1**	**LP2**	**WP2**	**LP3**	**WP3**	**LP4**	**WP4**	**LP4pr**	**LP4pas**	**LP4pa**	**LP4m**
IPS36759	Left	19.1	13.7	—	—	17.2	9.9	23.4	15.1	35.5	18.9	9.0	10.3	12.4	—
IPS36759	Right	20.1	13.4	5.5	6.1	16.4	9.7	23.5	14.0	35.1	17.9	9.4	—	—	12.3
IPS36758	Left	19.2	—	—	5.8	—	12.1	23.8	17.5	35.3	20.1	8.6	11.0	13.5	13
IPS36758	Right	—	—	—	—	18.3	12.5	23.8	16.5	35.4	18.9	8.4	10.2	13.1	12.6
IPS27340	Left	17.9	—	—	—	17.6	—	24.3	—	36.7	—	—	—	14	13.3
IPS27340	Right	16.1	—	—	—	18.1	—	22.9	—	35.8	—	—	—	12.6	12.4

Tab. 1 - Measurements (in mm) of the crania of *Pliocrocuta perreri* from Villarroya and La Puebla de Valverde. Abbreviations: PA, prosthion-acrocranion length; SKL, prosthion-occipital condyles length; PB, prosthion-basion length; SB, synsphenion-basion length; PS, prosthion-synsphenion length; FA, frontal-acrocranion length; PN, prosthion-nasion length; PF, prosthion-frontal length; PT, prosthion-staphylion length; LP1-P4, length of the upper premolar series; Woc, width of occipital condyles; WP4, palatal width at P4; WC, palatal width at C1; Hoc, occipital height; L, mesiodistal length; W, buccolingual width; LP4pr, mesiodistal length of fourth upper premolar protocone; LP4pas, mesiodistal length of fourth upper premolar parastyle; LP4pa, mesiodistal length of fourth upper premolar parastyle; LP4m, mesiodistal length of P4 metacone.

including the alveolar bone surrounding the tooth roots. The upper dentition is preserved except for the right P4, although the left P3 is misplaced (rotated) due to incorrect preparation. The mandible displays many fractures but is well preserved, except for some portions of the corpora and rami that have been reconstructed plaster. The lower dentition is completely preserved except for the right c1.

Measurements - See Tab. 1.

Description - The specimens reported here display an elliptic (higher than broad) nasal aperture as well as narrow triangular nasals, like *Hyaena* and *Parahyaena*. The nasal aperture is also wider than in *Crocuta*, more comparable to that of *Hyaena* and *Parahyaena*. The muzzle is long, with a very marked postcanine constriction, as in *Crocuta*. The frontomaxillary suture, as shown by IPS36759, is curved and posteriorly situated, most closely resembling in this regard both *Hyaena* and *Parahyaena*. The premaxillary suture, visible in IPS36759, does not reach the frontonasal suture, unlike in *Crocuta* and *Hyaena*, but are clearly separated as in *Parahyaena*. The marked postorbital processes display small lateral projections (only ascertainable in IPS36759 and IPS36758) as in *Crocuta*, whereas in *Hyaena* and *Parahyaena* these processes protrude basally. The tooth rows are markedly curved, as in *Crocuta* and *Parahyaena*. The palate, as seen in IPS36759 and IPS36758, is wide distally, thus resembling the condition in *Crocuta* and *Hyaena*. The basioccipital, observable in IPS36759 and IPS36758, more closely resembles that of *Parahyaena* in displaying a small central ridge as well as a transverse ridge at the beginning of the occipital condyles. The dorsal profile of the temporal region is slightly convex, with a degree of curvature intermediate between those of *Hyaena* (low curvature) and *Crocuta* (high curvature). The rostrum is relatively high and long (only preserved in IPS3658 and IPS36759), so that the nasals are more horizontally oriented than in extant bone-cracking hyenas. The anterior-most portion of the orbits is laterally situated at the level between P3 and P4, and the elliptical infraorbital foramen is situated at the level of the P3 protocone, as in the extant bone-cracking hyenas. The curvature of the nuchal crest (only well preserved in IPS36759) is marked, resembling the condition displayed by *Parahyaena*. In caudal view, the occipital outline (preserved in IPS36759 and IPS36758) is triangular, with marked nuchal and occipital crests, as in extant bone-cracking hyenas. The mandible is robust, as it is in the latter taxa.

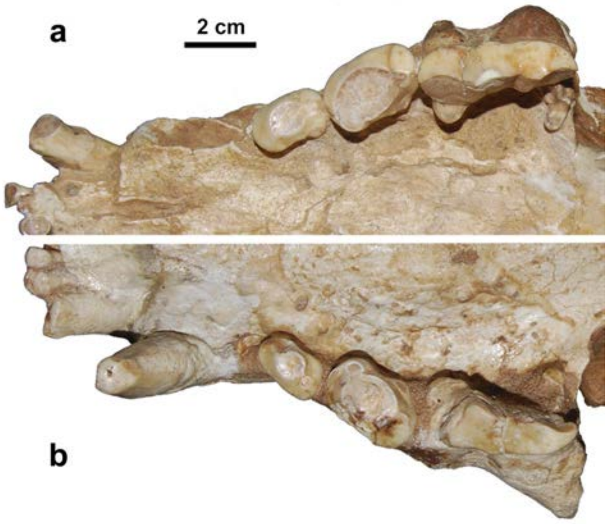

Fig. 3 - Tooth rows in *Pliocrocuta perrieri* in occlusal view. a) IPS36758, left tooth row; b) IPS36759, right tooth row.

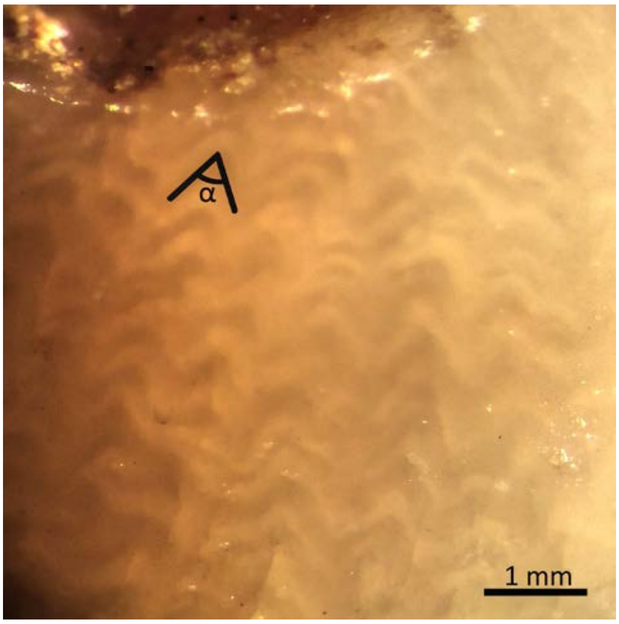

Fig. 4 - Stereomicroscope photograph of the marked zigzag pattern of the HSB on the outer enamel surface of the left P3 of *Pliocrocuta perrieri*. Note that α < 90º.

The dentition shows clear bone-cracking adaptations. The P1 is small and unicuspid, with a small buccal cingulum, as in extant bone-cracking hyenas (Fig. 3). The P2 displays a rectangular occlusal outline and bears two (mesial and distal) small but distinct accessory cusps, also as in extant bone-cracking hyenas. The P3 is stout (buccolingually broad) and displays well-developed accessory cusps, as in *Crocuta*, *Hyaena* and *Parahyaena,* the mesial cuspid being rotated lingually. The P4 displays a well-developed and mesiolingually-oriented protocone, which is slightly larger and more mesially situated in IPS27340, as well as a paracone of the same length as the metastyle. The M1 is present, being relatively large and displaying a rectangular occlusal outline. This tooth is buccolingually broader than mesiodistally long (Fig. 3), as in *Hyaena* and *Parahyaena*, thus differing from that of *Crocuta*, which is usually smaller and rounder (if present at all). The lower premolars display a rectangular occlusal outline. The p2 displays a medium-sized protocone and no mesial accessory cuspid. This tooth reaches its maximum width at the level of the posterior accessory cuspid, which is moderately developed, as in extant bone-cracking hyenas. The p3 lacks the mesial accessory cuspid, unlike *Hyaena*, and displays a well-developed protocone and a wide distal accessory cuspid, like *Parahyaena*. The p4 displays both mesial and distal accessory cuspids, as well as a well-developed protocone, as in extant bone-cracking hyenas. The mesial accessory cuspid is smaller than the distal cuspid, and situated on the lingual portion of the crown, being more developed than in *Crocuta*. In contrast, the p4 distal accessory cuspid is more mesially situated, thus resembling the condition of both *Hyaena* and *Parahyaena*. The m1 is rather small, with a long paraconid and a short protoconid. The buccal margin of the paraconid displays a small cingulid. The m1 talonid is long and bicuspid, contrasting with the short and unicuspid talonid of *Hyaena* and *Parahyaena*, as well as with the almost completely reduced talonid of *Crocuta*. The presence/absence of metaconid in the m1 cannot be ascertained.

Regarding enamel microstructure, due to preservational reasons, HSB were only observable on the outer enamel surface of two of the studied specimens (IPS36758 and IPS36759). They are well separated from one another and display a marked zigzag pattern (Fig. 4), with a mean angle α < 90º. This morphology is characteristic of the three extant bone-cracking hyenas and the extinct *Pachycrocuta*, clearly distinguishing the studied specimens from *Chasmaporthetes*, which displays less steeply folded bands that are more closely packed with one another (Ferretti, 1999).

Morphological comparisons - The morphology of the described specimens (IPS36759, IPS36758 and IPS27340) closely resembles that of the Saint-Vallier specimens (QSV20 and QSV48; Viret, 1954) in the following features: convex superior cranial profile with only a small concave depression at the frontonasal region; relatively long muzzle; short braincase not extended posteriorly by the sagittal crest; slender, long and triangular nasals lacking intermaxillary contact; maxillae barely elevated above the orbits; not markedly broad palate; robust anterior teeth relative to the cheek teeth; P1 present; relatively small P2; robust P3 with a high main cusp and mesial and distal crests; P4 with a large and high parastyle, an elongate metacone longer than the paracone, and a well-developed protocone that is not expanded towards the parastyle; and well-developed M1 with a marked parastyle lobe.

In spite of the similarities mentioned above, the studied specimens display several minor differences among them and/or compared with the Saint-Vallier material. Thus, the three described crania display a conspicuous postcanine constriction, which is less marked in one of the Saint-Vallier specimen (QSV20), and most developed in IPS27340. All the specimens possess postorbital processes with small lateral projections (except QSV48, which displays more marked projections). The occipital protuberance is proportionally more protruding in IPS36759. A markedly-developed P4 root is present in all the specimens, although it is less marked in QSV20 and IPS27340. The nasal fossa is slightly wider in QSV48 than in the other specimens. The curvature of the tooth rows is slightly variable, being least marked in QSV20, which further displays a narrower palate as well as narrower and more protruding occipital condyles than the remaining specimens. Dental differences among the various available specimens are minor, the most variable character being the position of P1. This tooth is situated between the canine and P2 in all the specimens except QSV48, in which it is more lingually situated (next to the distolingual aspect of the canine).

In contrast with the minor differences reported above, when compared with other skulls of *P. perrieri*, the described specimens (IPS36759, IPS36758 and IPS27340) display major differences compared with the sympatric hunting hyena *C. lunensis* (Viret, 1954; Antón et al., 2006; Ferretti, 2007) and the Early Pleistocene giant short-faced hyena *Pa. brevirostris* (Boule, 1893; Kretzoi, 1938; Werdelin & Sanders, 2010). Thus, the described crania differ from *C. lunensis* in the more anteriorly situated

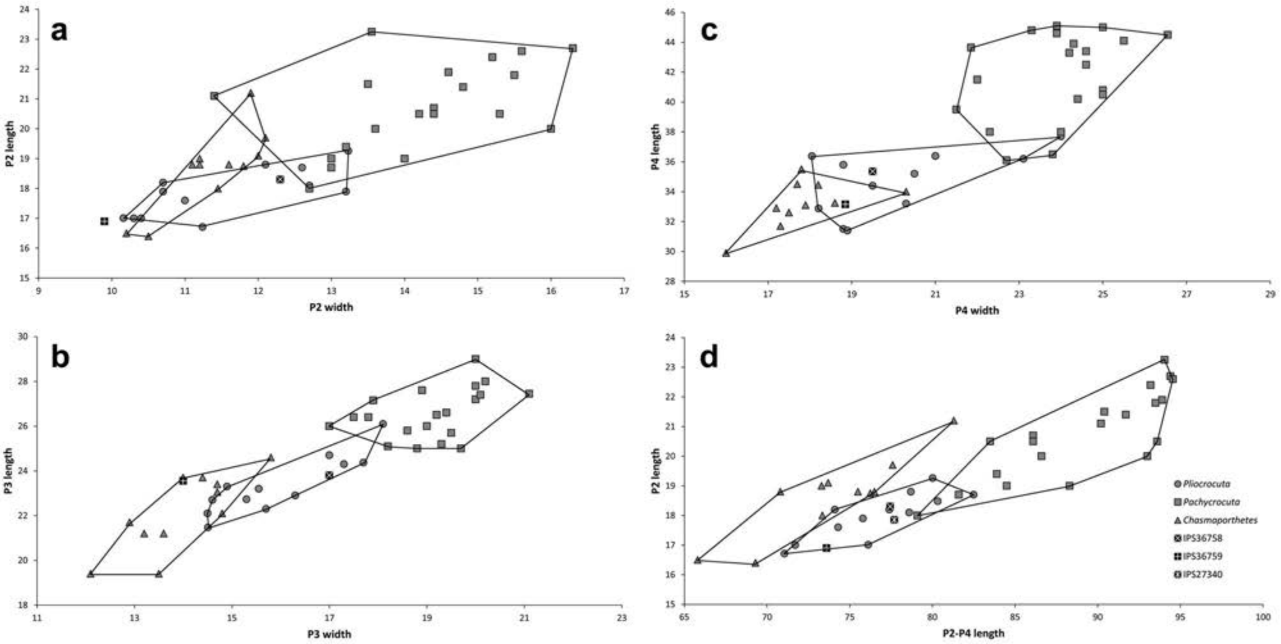

Fig. 5 - Bivariate plots of dental size and proportions in the described specimens of *Pliocrocuta perrieri*, compared to other specimens of this species as well as *Chasmaporthetes lunensis* and *Pachycrocuta brevirostris*. Hand-drawn polygons link the most extreme values of each species, to ease the visualization of metrical differences among them. a-c) Mesiodistal length vs. buccolingual width in the P2 (a), P3 (b) and P4 (c); d) P2 mesiodistal length vs. P2-P4 series length.

orbits, the more posterior infraorbital foramen, the more strongly developed postorbital process, the triangular nasals, the longer muzzle, the comparatively larger I3 and the steeply folded HSB with a marked zigzag pattern on the outer enamel surface. In turn, the described crania differ from *Pa. brevirostris* in the smaller overall size, the longer rostrum, the presence of mesial accessory cusps in the P2 and P3, the less developed premolar protocones, and the slenderer P4 paracone.

Morphometric comparisons - The size and proportions of the premolars in the described specimens are compared to those of previously-known specimens of *P. perrieri*, *C. lunensis* and *Pa. brevirostris* in Fig. 5. Standard bivariate plots of width vs. length of the upper premolars (P2-P4; Fig. 5a-c) overlap to some degree among the various species in all instances, with *Pa. brevirostris* displaying largest absolute dimensions for the three premolars. For both the P3 (Fig. 5b) and the P4 (Fig. 5c), *P. perrieri* shows similar proportions but intermediate sizes between *C. lunensis* (smaller) and *Pa. brevirostris* (larger), only with some overlap. For the P2 (Fig. 5a), *Pa. brevirostris* overlaps more extensively with *C. lunensis* in length, although many specimens of the latter tend to display a relatively wider P2. Among the studied specimens, IPS36758 exclusively overlaps with the scatter of *P. perrieri* (thus confirming the attribution to this taxon), whereas IPS36759 does not overlap with any of the studied hyaenid species for the P2 (falling close to both *P. perrieri* and *C. lunensis*), overlaps with both *P. perrieri* and *C. lunensis* for the P3, and overlaps only with *C. lunensis* for the P4. Overall, upper premolar proportions are not reliable for providing a secure taxonomic attribution, since they do not enable a clear and unambiguous discrimination among these taxa.

In contrast, the length of the P2 relative to the P2-P4 row provides a much better discrimination among the three studied species (Fig. 5d), since the P2 of *P. perrieri* is relatively shorter than in *C. lunensis*, only with a very minimal overlap. *Pachycrocuta brevirostris*, in turn, differs from both *P. perrieri* and *C. lunensis* by the larger dental size of the former, with only a very minimal overlap with the largest specimens of *P. perrieri*. Regarding this feature, all the studied specimens (further including IPS27340, for which premolar width is not available) exclusively overlap with *P. perrieri*, thus supporting our taxonomic attribution to this taxon on the basis of qualitative morphological features.

The DA (Tab. 2 and Fig. 6) yields two discriminant functions (DF), with a Wilk's lambda significant at $p<0.001$ (DF1) and $p<0.01$ (DF2). Based on these functions, the analysis provides a very good discrimination between the three extinct hyaenids included, by correctly classifying 95.2% of the original cases (85.7% when cross-validation is employed). DF1 separates *Pachycrocuta* (positive values) from both *Pliocrocuta* (generally rather negative values, only minimally overlapping with *Pachycrocuta*) and *Chasmaporthetes* (highly negative values, with no overlap with *Pachycrocuta*), being mostly driven by size (especially P3 width and P4 length). DF2, in turn, mostly discriminates between *Pliocrocuta* (negative values) and *Chasmaporthetes* (positive values), with *Pachycrocuta* displaying values around zero that largely overlap with the two other taxa. This axis is mostly driven by P2 length and width (the larger the P2, the more positive the values along DF2) as well as P3 width (the wider the P2, the more negative the values along DF2). The analysis therefore shows that *Pliocrocuta* dentally differs from *Pachycrocuta* mostly by displaying smaller teeth, whereas in contrast

Canonical discriminant functions		
	DF1	**DF2**
Eigenvalue	5.587	0.549
% of Variance	91.1	8.9
Cumulative %	91.1	100.0
Canonical Correlation	0.921	0.595
Standardized discriminant coefficients		
	DF1	**DF2**
LP2	-0.392	0.863
WP2	-0.417	0.754
LP3	-0.092	0.133
WP3	0.693	-0.701
LP4	0.678	-0.116
WP4	0.435	-0.079
Structure matrix		
	DF1	**DF2**
LP4	0.838	0.187
WP3	0.788	0.173
WP4	0.682	0.594
LP3	0.629	0.304
WP2	0.340	0.812
LP2	0.466	0.626
Functions at group centroids		
	DF1	**DF2**
Pliocrocuta	-0.814	-1.171
Pachycrocuta	2.210	0.284
Chasmaportetes	-3.204	0.654
Discriminant scores		
	DF1	**DF2**
IPS36758	-0.606	-0.955
IPS36759	-2.030	-1.313

Tab. 2 - Results of the canonical variate Discriminant Analysis (see also Fig. 4a) based on dental measurements for previously-known specimens of *Pliocrocuta perrieri*, *Chasmaporthetes lunensis* and *Pachycrocuta brevirostris*. The specimens described here were left ungrouped and classified a posteriori by the analysis.

it differs from *Chasmaporthetes* by dental proportions (especially the smaller P2 and the stouter P3).

With regard to the new crania described here, the analysis classifies them both as *Pliocrocuta* in first instance, with a classification probability of p=0.956 for IPS36758 and p=0.473 for IPS36759 (and posterior probabilities of p=0.981 and p=0.867, respectively); as a second alternative, the new skulls are classified as *Chasmaporthetes*, with much lower posterior probabilities (p=0.010 in IPS36758 and p=0.133 in IPS36759). This can be clearly seen in the plot of DF2 versus DF1 (Fig. 6), in which the two described crania are much closer to the *Pliocrocuta* centroid (Mahalanobis squared distances of $D^2=0.09$ for IPS36758 and $D^2=1.498$ for IPS36759) than to that of *Chasmaporthetes* ($D^2=9.34$ and $D^2=5.248$, respectively).

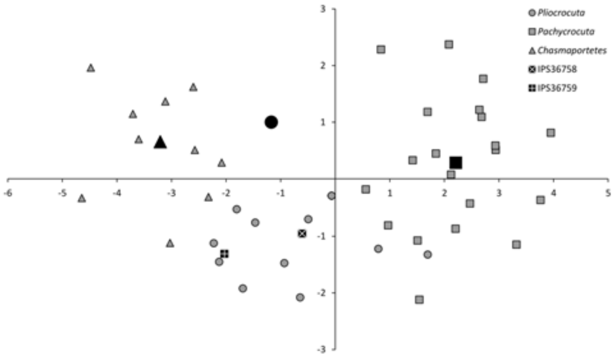

Fig. 6 - Bivariate plot of both individual scores (small gray symbols) and group centroids (larger black symbols) for the first two discriminant functions, obtained from the canonical variate Discriminant Analysis performed on the basis of the mesiodistal length and buccolingual width of the upper premolars in IPS36758 and IPS36759, compared to individuals of *Pliocrocuta perrieri*, *Chasmaporthetes lunensis* and *Pachycrocuta brevirostris* from other localities.

Artistic reconstruction - In Fig. 7 we provide a reconstruction of the skull and life appearance of the head of *Pliocrocuta perrieri*, which is mainly based on the crania described here, further complemented (when necessary to reconstruct areas damaged in the described specimens) by data from the Saint-Vallier specimens QSV20 and QSV48 (Viret, 1954).

DISCUSSION AND CONCLUSIONS

The studied hyaenid skulls from Villarroya and La Puebla de Valverde closely resemble the previously-known material of *Pliocrocuta perrieri* (Viret, 1954; Howell & Petter, 1980) in both cranial morphology (e.g., relatively long muzzle, short braincase, slender and triangular nasals) and dental features (presence of P1 and broad premolars, with a relatively short P2). In contrast, the described material displays marked differences compared with both *Chasmaporthetes lunenis* (shorter muzzle, more anterior orbits, more posterior infraorbital foramen, triangular nasals, stouter upper premolars with a relatively shorter P2, and zigzag pattern of HSB on tooth enamel) and *Pa. brevirostris* (including smaller cranial and dental size, longer muzzle, less developed premolar protocones and several occlusal details). An attribution to *P. perrieri* of the described specimens is further confirmed by the multivariate analyses performed here based on dental size and proportions.

The described skulls show some degree of intraspecific variability in various craniodental features, both among themselves and/or compared with specimens from other localities. These features include the development of the postcanine constriction, the projection of the postorbital processes, the occipital protuberance and the occipital condyles, the development of the P4 root, the width of the nasal aperture and the palate, and the position of the P1. Such differences are however very minor (compared

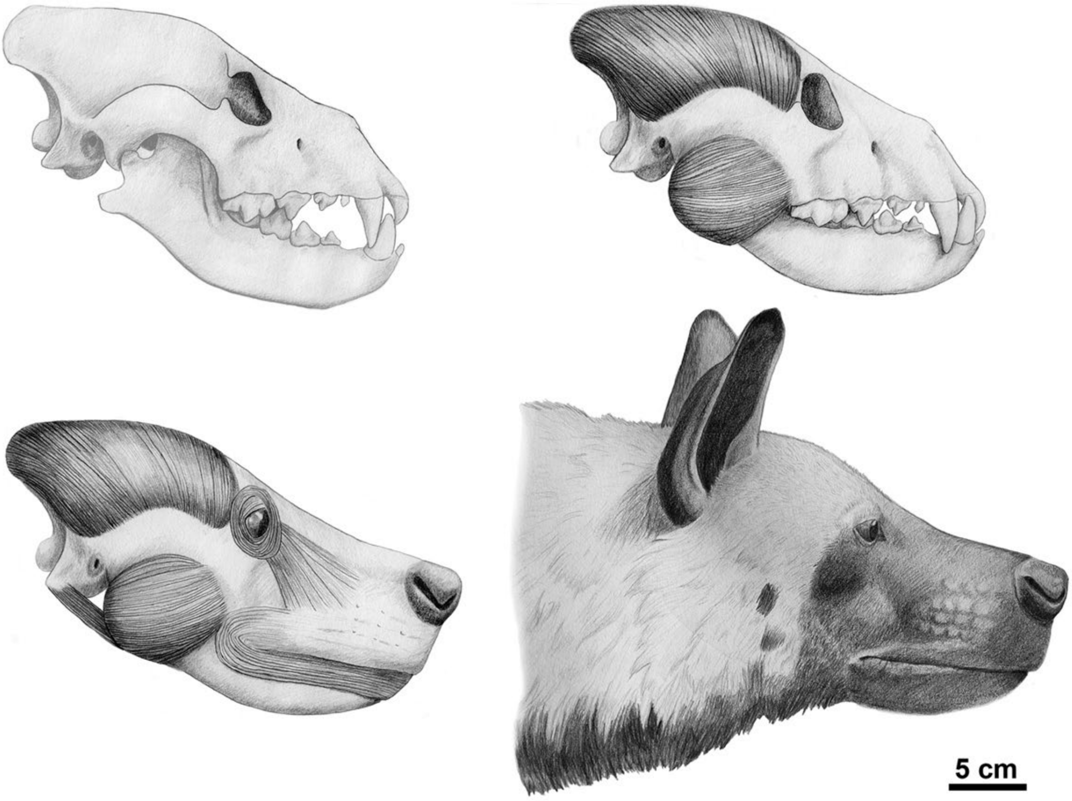

Fig. 7 - Artistic reconstruction of the skull and life appearance of *Pliocrocuta perrieri*, mainly based on the material from Villarroya (IPS36759 and IPS36758) and La Puebla de Valverde (IPS27340).

to the differences between *P. perrieri* and other hyaenid taxa) and do not merit any taxonomic value. The skulls of *P. perreri* described here therefore enable to better evaluate the intraspecific variability in cranial morphology in this taxon, for which relatively complete adult skulls were only previously known from the locality of Saint-Vallier. Overall, the Iberian material of *P. perrieri* confirms that, in spite of some degree of variation in cranial features, this taxon consistently differs in craniodental morphology from both the contemporaneous hyena *C. lunensis* and its purported descendant *Pa. brevirostris*. Moreover, the future study of the internal cranial anatomy of the new specimens of *P. perrieri* described here may shed new light on the paleoecology and phylogenetic relationships of this taxon compared to the extant and other extinct bone-cracking hyenas.

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REFERENCES

Adrover R., Aguirre E., Heintz E., Moissenet E. & Morales J. (1974). Formaciones plio-pleistocenas del Llano de Sarrión. *In* Aguirre E. & Morales J. (eds), Coloquio internacional sobre biostratigrafia continental del Neógeno superior y cuaternario inferior, libro guía: 69-83.

Adrover R. & Soria D. (1976). Hallazgo de *Hyaena donnezani* Viret en La Calera II (Aldehuela, provincia de Teruel). *Teruel: Revista del Instituto de Estudios Turolenses*, 55: 189-205.

Agustí J. & Oms O. (2001). On the age of the last hipparionine faunas in western Europe. *Comptes Rendus de l'Académie des Sciences de Paris*, 332: 291-297.

Alba D.M., Vinuesa V. & Madurell-Malapeira J. (in press). On the original author and year of description of the extinct hyaenid *Pachycrocuta brevirostris*. *Acta Palaeontologica Polonica*. http://dx.doi.org/10.4202/app.00017.2013

Alberdi M.T., Azanza B., Cerdeño E. & Prado J.L. (1997). Similarity relationship between mammal faunas and biochronology from Latest Miocene to Pleistocene in the Western Mediterranean área. *Eclogae Geologicae Helvetiae*, 90: 115-132.

Alcalá L. (1994). Macromamíferos neógenos de la fosa de Alfambra-Teruel. Ph.D. dissertation. 554 pp. Instituto de estudios Turolenses y Museo Nacional de Ciencias Naturales, Consejo superior de Investigaciones Cíentificas, Madrid.

Anadón P., Utrilla R., Vázquez A., Martín-Rubio M., Rodriguez-Lázaro J. & Robles F. (2009). Paleoenviromental evolution of the Pliocene Villarroya lake, northern Spain, from stable isotopes and trace-element geochemistry of ostracods and mollusks. *Journal of Paleolimnology*, 39: 339-419.

Antón M., Turner A., Salesa M.J. & Morales, J. (2006). A complete skull of *Chasmaporthetes lunensis* (Carnivora, Hyaenidae) from the Spanish Pliocene site of La Puebla de Valverde (Teruel). *Estudios Geológicos*, 62: 375-388.

Argant A. (2004). Les Carnivores du gisement Pliocène final de Saint-Vallier (Drôme, France). *Geobios*, 37: 133-182.

Arribas A. & Palmqvist P. (1999). El modelo de actividad de *Pachycrocuta* en Venta Micena: implicación de los hiénidos en el registro paleomastológico Plio-Pleistoceno español. *Temas Geológicos-Mineros*, 26: 173-181.

Arribas Herrera A. & Bernad García J. (1994). Catálogo de mamíferos pliocenos del yacimiento de Villarroya (La Rioja), en la colección del Museo Geominero. *Boletín Geológico y Minero*, 105: 236-248.

Baryshnikov G.F. & Tsoukala E. (2010). New analysis of the Pleistocene carnivores from Petralona Cave (Macedonia, Greece) based on the Collection of the Thessaloniki Aristotle University. *Geobios,* 43: 389-402.

Boule M. (1893). Description de l'*Hyaena brevirostris* du Pliocène de Sainzelles près le Puy (Haute-Loire). *Annales des sciences naturelles. Zoologie et paléontologie*, 15: 85-97.

Bowditch T.E. (1821). An analysis of the natural classifications of Mammalia for the use of students and travelers. 155 pp. J. Smith, Paris.

Carvajal E. (1926). Nota sobre un yacimiento de fósiles vertebrados en el Plioceno de la provincia de Logroño. *Boletín del Instituto Geológico y Minero de España*, 47: 317-333.

Croizet J.B. & Jobert A.C.G. (1828). Recherches sur les Ossements Fossiles du Département du Puy-de-Dôme. 224 pp. Delahays, Paris.

Crusafont Pairó M., Hartenberger J.L. & Heintz E. (1964). Un nouveau gisement de Mammifères fossiles d'âge villafranchien à La Puebla de Valverde (Province de Teruel, Espagne). *Comptes Rendus hebdomadaires des séances de l'Académie des Sciences*, 258: 2869-2871.

Del Campana D. (1914). La *Lycyaena lunensis* n. sp. dell'ossario pliocenico di Olivola (Val di Magra). *Palaeontographia Italica*, 20: 87-104.

Depéret C. (1890). Animaux Pliocènes du Rousillon. *Mémoires de la Société géologique de France. Paléontologie*, 3: 1-194.

De Serres M., Dubreuil J. & Jeanjean B. (1828). Mémoires sur diverses espècies d'hyènes fossiles découvertes das les cavernes de Lunel-Viel. *Memóires du Muséum National d'histoire Naturelle*, 17: 269-312.

Ferretti M.P. (1999). Tooth enamel structure in the hyaenid *Chasmaporthetes lunensis lunensis* from the Late Pliocene of Italy, with implications for feeding behavior. *Journal of Vertebrate Paleontology*, 19: 767-770.

Ferretti M.P. (2007). Evolution of bone-cracking adaptions in hyaenids (Mammalia, Carnivora). *Swiss Journal of Geosciences*, 100: 41-52.

Ficcarelli G. & Torre D. (1970). Remarks on the taxonomy of hyaenids. *Palaeontographia Italica*, 66: 13-33.

Gautier F. & Heintz E. (1974). Le gisement villafranchien de La Puebla de Valverde (Province de Teruel, Espagne). *Bulletin du Muséum d'Histoire Naturelle*, 228: 113-133.

Geraads, D. (1997). Carnivores du Pliocène terminal de Ahl al Oughlam (Casablanca, Maroc). *Geobios*, 30: 127-164.

Gervais P. (1848-1852). Zoologie et Paléontologie Françaises. Nouvelles Recherches sur les Animaux Vivants et Fossiles de la France. Tome I. Contenant l'Énumération Méthodique et Descriptive des Espèces ainsi que les Principes de leur Distribution Géographique et Paléontologique. 271 pp. Arthus Bertrand, Paris.

Gray J.E. (1821). On the natural arrangement of vertebrose animals. *London Medical Repository*, 15: 296-310.

Howell F.G. & Petter G. (1980). The *Pachycrocuta* and *Hyaena* lineages (Plio-Pleistocene and extant species of the Hyaenidae). Their relationships with Miocene ictitheres: *Palhyaena* and *Hyaenictitherium*. *Geobios*, 13: 579-623.

Jiménez García S., Martín de Jesús S. & Jiménez Fuentes E. (1999). Primeros resultados de la excavación "Villarroya 88-89". *Studia Geológica Salmanticensia*, 35: 569-572.

Koenigswald W.V. & Sander P.M. (1997). Tooth enamel microstructure. 280 pp. Balkema, Rotterdam.

Kretzoi M. (1938). Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtfauna. (Ein Beitrag zur Stratigraphie des Altquartärs). *Annales Historico-Naturales Musei Nationalis Hungarici*, 31: 88-157.

Madurell-Malapeira J. (2010). The Villafranchian carnivores from the North-Eastern Iberian Peninsula and the Early-Middle Pleistocene Transition. 224 pp. Ph.D. dissertation, Universitat Autònoma de Barcelona.

Olive F. (2006). Évolution des grands Carnivores au Plio Pléistocène en Afrique et en Europe occidentale. *L'Anthropologie*, 110: 850-869.

Qiu Z. (1987). Die Hyaeniden aus dem Ruscinium und Villafranchium Chinas. *Münchner Geowissenschaftliche Abhandlungen A*, 9: 1-108.

Rook L., Ferretti M.P., Arca M. & Tuveri C. (2004). *Chasmaporthetes melei* n.sp., an endemic hyaenid (Carnivora, Mammalia) from Monte Tuttavista fissure fillings (late Pliocene to early Pleistocene; Orosei, Sardinia, Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 110: 707-718.

Sinusía C., Pueyo E.L., Azanza B. & Pocoví A. (2004). Datación magnetoestratigráfica del yacimiento paleontológico de Puebla de Valverde (Teruel). *GeoTemas*, 6: 339-342.

Turner A. (1990). The evolution of the guild of larger terrestrial carnivores in the Plio-Pleistocene of Africa. *Geobios*, 23: 349-368.

Turner A. (2001). Remains of *Pachycrocuta brevirostris* (Mammalia, Hyaenidae) from the Lower Pleistocene site of Untermassfeld near Meiningen. *In* Kahlke H.D. & Kahlke R.D. (eds), Das Pleistozän von Untermassfeld in Thuringen: 673-690: Rudolf Harbelt Verlag, Bonn.

Turner A., Antón M. & Werdelin L. (2008). Taxonomy and evolutionary patterns in the fossil Hyaenidae of Europe. *Geobios*, 41: 677- 687.

Villalta Comella J.F. (1952). Contribución al conocimiento de la fauna de mamíferos fósiles del Plioceno de Villarroya (Logroño). *Boletín del Instituto Geológico y Minero de España*, 64: 1-203.

Viret J. (1954). Le loess à bancs durcis de Saint-Vallier (Drôme) et sa faune de mammifères villafranchiens. *Nouvelles archives du Muséum d'histoire naturelle de Lyon*, 4: 1-200.

Werdelin L. & Lewis M.E. (2012). The taxonomic identity of the type specimen of *Crocuta sivalensis* (Falconer, 1867). *Journal of Vertebrate Paleontology*, 32: 1453-1456.

Werdelin L. & Sanders W.J. (2010). Cenozoic mammals of Africa. 986 pp. University of California Press, California.

Werdelin L. & Solounias N. (1991). The Hyaenidae: taxonomy, systematics and evolution. *Fossils and Strata*, 30: 1-104.

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Chapter 6. Ursidos, hiénidos y félidos del Pleistoceno Inferior de Cueva Victoria (Cartagena, Murcia)

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Summary: This work describes the carnivoran faunal assemblage of Cueva Victoria other than canids. The hyaenid described in this work is *Pachycrocuta brevirostris*, which is compared with other specimens of this species from elsewhere in Eurasia.

Author's contribution: The doctoral candidate participates in work as a coauthor (3rd position). He described and compared the hyaenid remains from the site, made the figures, and revised the whole manuscript.

Úrsidos, hiénidos y félidos del Pleistoceno inferior de Cueva Victoria (Cartagena, Murcia)

Early Pleistocene ursids, hyaenids and felids from Cueva Victoria (Cartagena, Murcia)

J. Madurell-Malapeira*
J. Morales**
V. Vinuesa*
A. Boscaini*

Resumen

En este trabajo se hace la revision de la colección de carnívoros fósiles del yacimiento de Cueva Victoria (sureste de la Península Ibérica), incluyendo las familias Ursidae, Hyaenidae y Felidae. El material estudiado incluye las especies *Ursus deningeri, Pachycrocuta brevirostris, Homotherium latidens, Megantereon* sp., *Panthera gombaszoegensis, Puma pardoides* y *Lynx pardinus*. Estas especies son características de las asociaciones del Pleistoceno Inferior tardío de la Europa mediterránea y corresponden al biocrón Epivillafranquiense, con una edad aproximada de 1,1-0,78 Ma.

Teniendo en cuenta los datos conocidos de los últimos y primeros registros conocidos de las especies *U. deningeri, L. pardinus* y *Megantereon,* esta cronología se podría precisar en torno a ca. 1 Ma.

Abstract

In this paper we review the collection of fossil carnivores from the late Early Pleistocene site of Cueva Victoria (south-eastern Iberian Peninsula) including the families Ursidae, Hyaenidae and Felidae. The studied material includes the species *Ursus deningeri, Pachycrocuta brevirostris, Homotherium latidens, Megantereon* sp., *Panthera gombaszoegensis, Puma pardoides* and *Lynx pardinus*. The former species are characteristic of the late Early Pleistocene assemblages of the Mediterranean Europe corresponding to the Epivillafranchian biochron with an approximate age of 1.1-0.78 Ma. Taking into account the known first and last appearances of the identified species the chronology of the site can be restricted to ca. 1.0 Ma.

* Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona. Edifici ICTA-ICP, c\ de les columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona: Joan.madurell@icp.cat; victor.vinuesa@icp.cat; alberto.boscaini@icp.cat
**Museo Nacional de Ciencias Naturales-Consejo Superior de Investigaciones Científicas (MNCN-CSIC), Madrid, Spain: jorge.morales@mncn.csic.es

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INTRODUCCIÓN

Las primeras noticias sobre hallazgos paleontológicos en Cueva Victoria se remontan a 1970, cuando en las actas del primer congreso Nacional de Espeleología celebrado en Barcelona se cita la presencia de un yacimiento con diversos restos atribuidos a *Equus stenonis, Equus caballus* y *Hipparion* (Valenzuela, 1970). En 1977, Joan Pons-Moyà durante una estancia en Cartagena redescubre el yacimiento de Cueva Victoria, iniciando los primeros trabajos en él. En 1978 se publica el primer trabajo sistemático basado en las faunas fósiles de Cueva Victoria, en este caso concerniente a la asociación de carnívoros (Pons-Moyà y Moyà-Solà, 1978), en el se describen los restos de carnívoros encontrados hasta la fecha estimando una edad de Pleistoceno medio (Mindel inferior) para la asociación (Tabla 1). El año 1979 se llevan a cabo los primeros trabajos sistemáticos en Cueva Victoria con un equipo formado por el mismo Joan Pons-Moyà, Salvador Moyà-Solà, Josep Fernández de Villalta, Jordi Agustí y Eudald Carbonell. Durante esta campaña se descubren los primeros indicios de supuesta presencia humana en el yacimiento, proporcionando por primera vez una lista faunística preliminar de los restos de mamíferos localizados en el yacimiento (Carbonell et al., 1981; Tabla 1). Con los nuevos datos aportados en este trabajo se concluye que la edad de la acumulación pertenece al Pleistoceno inferior, en concreto al rango 1.3-0.9 Ma (Carbonell et al., 1981). Simultáneamente al anterior trabajo, Joan Pons-Moyà publica el primer estudio exhaustivo sobre uno de los taxones de carnívoros del yacimiento, en este caso, *Canis etruscus* (Pons-Moyà, 1981). El trabajo exhaustivo de Pons-Moyà sobre los taxones de carnívoros de Cueva Victoria es seguido por dos publicaciones más centradas en el estudio de los restos de *Pachycrocuta brevirostris* y *Lynx spelaea* (Pons-Moyà, 1982, 1983). La datación de los restos da lugar a nuevos trabajos sobre la asociación de roedores, que confirman una edad estimada para la acumulación próxima a 1 Ma. (Alcalde et al., 1981; Agustí, 1982).

Desde 1984 un equipo liderado por el profesor Josep Gibert realiza numerosas excavaciones en el yacimiento, continuando estos trabajos hoy en día. De la larga lista de publicaciones realizadas desde entonces destacan dos monografías publicadas sobre las investigaciones en la Cuenca de Guadix-Baza y en Cueva Victoria (Gibert et al., 1989; Gibert, 1992). En trabajos posteriores se comparan las asociaciones de mamíferos identificadas con otras asociaciones Europeas y africanas permitiendo precisar la cronología alrededor de 1.5 Ma. (Gibert, 1999, 2004). Aunque en todos estos trabajos no se revisa sistemáticamente la asociación de carnívoros si que se aportan nuevas listas faunísticas del yacimiento (Tabla 1).

Gibert et al. (2006) proporcionan la última síntesis de datos geológicos, paleontológicos y magnetoestraigráficos sobre Cueva Victoria, concluyendo que la cronología de la acumulación es cercana a 1.4 Ma. Ahora bien, en un reciente trabajo sobre los restos de arvicólidos recuperados del yacimiento (Martin, 2012) y en base a nuevos datos magnetoestratigráficos y bioestratigráficos se concluye que la edad de la acumulación se situaría en el rango 0.98-0.78 Ma (Martin, 2012).

En el presente trabajo se estudian los restos de carnívoros, exceptuando los cánidos, extraídos en Cueva Victoria, tanto en las campañas históricas lideradas por Joan Pons-Moyà, como en las excavaciones posteriores lideradas por Josep Gibert.

METODOLOGÍA

Abreviaturas

IPS, colecciones del Institut Català de Paleontologia M. Crusafont, Universitat Autònoma de Barcelona; ; **IMEDEA**, colecciones del Institut Mediterrani d'Estudis Avançats; **MC**, colecciones del Museo Arqueológico Municipal de Cartagena.

Material estudiado

Los materiales descritos en este artículo proceden de tres instituciones diferentes. El material depositado en el Institut Català de Paleontologia M. Crusafont y en el Institut Mediterrani d'Estudis Avançats procede de las excavaciones realizadas por Joan Pons-Moyà, formaba parte de la colección personal del mismo, y fue cedido a estas dos instituciones tras su desafortunado fallecimiento. Las colecciones del Museo de Arqueología Municipal de Cartagena proceden de las excavaciones realizadas por Josep Gibert a partir de 1984. Alternativamente, también se ha estudiado la colección de Cueva Victoria depositada en el Museo de Geología de Barcelona, perteneciente a la colección personal, procedente

Pons-Moyà y Moyà-Solà, 1978	Carbonell et al., 1981	Pons-Moyà, 1983	Gibert et al., 1988	Ferrández et al., 1989
			Ursus etruscus	*Ursus etruscus*
Canis etruscus	*Canis etruscus*		*Canis etruscus arnensis*	*Canis etruscus arnensis*
Cuon rosi	*Xenocyon rosi*		*Xenocyon rosi*	*Xenocyon rosi*
	Vulpes sp.		*Vulpes* sp.	*Vulpes* sp.
Hyaena brevirostris	*Pachycrocuta brevirostris*		*Pachycrocuta brevirostris*	*Pachycrocuta brevirostris*
			Homotherium crenatidens	*Homotherium crenatidens*
Machairodontidae indet.	*Megantereon* sp.		*Megantereon* sp.	*Megantereon* sp.
cf. *Jansofelis* sp.	*Panthera gombaszoegensis*		*Panthera gombaszoegensis*	*Panthera gombaszoegensis*
Felis aff. *toscana*				
	Viretailurus schaubi			
	Acinonyx sp.			
Felis (Lynx) sp.	*Lynx* sp.	*Lynx spelaea*	*Lynx*sp.	*Lynx* sp.
	Carnivora indet.			
Gibert et al., 1995	**Gibert, 1999**	**Gibert et al., 2006**	**Blain et al., 2008**	
	Ursus sp.	*Ursus* cf. *etruscus*	*Ursus* cf. *U. etruscus*	
Canis etruscus	*Canis etruscus*	*Canis etruscus etruscus*	*Canis etruscus*	
Canis (Xenocyon) lycaonoides	*Canis falconeri*	*Xenocyon lycaonoides*	*Xenocyon lycaonoides*	
Vulpes sp.		*Vulpes* sp.	*Vulpes* sp.	
		Mustela sp.	*Mustela* sp.	
Pachycrocuta brevirostris	*Pachycrocuta brevirostris*	*Pachycrocuta brevirostris*	*Pachycrocuta brevirostris*	
Homotherium crenatidens	*Homotherium* sp.	*Homotherium crenatidens*	*Homotherium crenatidens*	
Megantereon cultridens	*Megantereon* sp.	*Megantereon* cf. *cultridens*	*Megantereon* cf. *M. cultridens*	
Panthera gombaszoegensis	*Panthera* sp.	*Panthera gombaszoegensis*	*Panthera onca gombaszoegensis*	
Panthera schaubi		*Viretailurus schaubi*	*Puma pardoides*	
Acinonyx sp.				
Lynx spelaeus	*Lynx* sp.	*Lynx spelaea*	*Lynx spelaea*	
	Felis sp.			
	Monachus monachus	*Phoca* sp.		

Tabla 1. Listas faunísticas de la asociación de carnívoros de Cueva Victoria aparecidas en las diferentes publicaciones realizadas hasta la fecha.

de la excavación de 1979, de J. F. de Villalta y posteriormente cedida a esta institución. En este último material no se han identificado restos de carnívoros.

PALEONTOLOGÍA SISTEMÁTICA

ORDEN Carnivora Bowdith, 1821
FAMILIA URSIDAE Gray, 1825
GÉNERO *Ursus* Linnaeus, 1758
ESPECIE ***Ursus deningeri*** **Von Reichenau, 1904**

Material: MC(CV-MC-105), fragmento mesial de m2 derecho; MC(CV-MC-89), primer metatarsiano izquierdo; MC(CV-MC-254), primera falange derecha con epífisis proximal incompleta.

Medidas: Tabla 2.

Descripción:

Dentición: Se ha podido identificar un solo resto dental de úrsido (MC(CV-MC-105), correspondiente a un germen de trigónido derecho de m2 que conserva protocónido y metacónido (Fig. 1F). El metacónido presenta una única cúspide principal, mostrando además dos pequeñas cúspulas accesorias, una mesial y otra distal, siendo la primera de mayor tamaño. El protocónido es simple y unicuspidado.

Restos postcraneales*:* Dos restos postcraneales atribuibles a úrsido han sido identificados. El primero, es un primer metatarsiano izquierdo (MC(CV-MC-89), que posee la diáfisis relativamente larga, robusta y recta (Fig. 1A,B). La epífisis proximal presenta la superficie articular proximal convexa dividida antero-posteriormente en dos zonas unidas por una inflexión, con la zona anterior muy

Especie	Nºinventario	Elemento	Lat.	L	DTP	DTM	DTD	DAPP	DAPM	DAPD
Ursus deningeri	MC(CV-MC-89)	MttI	Izq.	67.8	26.5	14.1	20.8	20.7	11.4	17.0
Ursus deningeri	MC(CV-MC-254)	Falange prox.	Der.	44.9		14.3	16.7	16.9	11.1	12.2
P. brevirostris	IMEDEA-C40a	MtcIII	Der.		17.8	13.5		23.4	11.3	
P. brevirostris	MC(CV-D-59)	Falange distal	Der.	24.5	13.6			17.3		
P. brevirostris	IMEDEA-C39a	Falange distal	Izq.	39.7	13.2			25.6		
H. latidens	IMEDEA-C40b	MttII	Der.	97.4	13.9	11.7	18.9		12.0	16.2
P. gombaszoegensis	IMEDEA-C39b	Falange prox.	Izq.	25.8	17.1		13.3	13.1		10.6
P. gombaszoegensis	IPS43404	Falange medial	Izq.	27.5	14.3		13.5	13.8		10.0
L. pardinus	IMEDEA-C40d	Húmero	Der.				30.2			18.3
L. pardinus	IMEDEA-C40c	Radio	Izq.		14.8			11.0		
L. pardinus	MC (CV-MC-162)	Radio	Izq.			12.7	24.4		8.3	14.8
L. pardinus	IMEDEA-C32a	MtcV	Izq.	48.9	9.5	6.5	8.9	9.9	5.1	7.6
L. pardinus	IMEDEA-C27c	Tibia	Der.				23.3			14.3
L. pardinus	MC (CV-D81)	Tibia	Der.				21.2			13.5
L. pardinus	MC (CV-MC-132)	Tibia	Der.			11.2	20.0		12.9	15.1
L. pardinus	IMEDEA-C40e	MttIII	Izq.		12.2	9.4		15.5	6.6	
L. pardinus	IMEDEA-C32b	MttV	Der.	70.6	9.0	5.1	8.2	10.6	5.4	7.6
L. pardinus	IMEDEA-C32c	Falange prox.	Izq.	21.3	8.8		7.4	7.8		5.8
L. pardinus	IMEDEA-C32d	Falange prox.	Der.	20.8	8.2		6.5	7.3		5.2
L. pardinus	MC (CV-MC-169)	Falange medial	Der.	17.6	7.3		7.0	7.7		6.1

Tabla 2. Medidas biométricas de diferentes elementos post-craneales de las especies de carnívoros registradas en Cueva Victoria. Abreviaturas: L, longitud proximo-distal; DTP, diámetro transversal proximal; DTM, diámetro transversal de la diáfisis; DTD, diámetro transversal distal; DAAP; diámetro antero-posterior proximal; DAPM, diámetro antero-posterior de la diáfisis; DAPD, diámetro antero-posterior distal.

inclinada en sentido antero-distal y la posterior prácticamente horizontal (Fig. 1C). El segundo resto corresponde a una falange proximal con la epífisis proximal incompleta (MC(CV-MC-254), cuya superficie articular proximal es fuertemente cóncava e inclinada en sentido antero-posterior. La diáfisis es corta y proporcionalmente robusta, presentando la curvatura dorso-palmar moderada (Fig. 1D,E).

Discusión:

Antecedentes: Los úrsidos del Villafranquiense final (ca. 1.8-1.2 Ma) han sido adscritos históricamente, así como en trabajos recientes, a la especie *Ursus etruscus* Cuvier, 1823. Entre ellos están los restos de Olivola, Upper Valdarno, Monte Argentario y Pirro Nord en Italia (Petrucci y Sardella, 2009; Petrucci et al., 2013), 'Ubeidiya en Israel (Ballesio, 1986; Martínez-Navarro et al., 2009), Venta Micena en la Península Ibérica (Torres, 1992; Palmqvist et al., 2005; Petrucci et al., 2013) y Ceyssaguet en Francia (Tsoukala, 2004).

Ahora bien, los úrsidos del Epivillafranquiense (ca. 1,1-0.8 Ma) han sido y son foco de controversias taxonómicas y filogenéticas. En 1992, la primera revisión precisa de los restos de grandes mamíferos localizados en la cueva francesa de Vallonnet (ca. 1.0 Ma) (Moullé, 1992) pone de manifiesto que los restos de úrsidos estudiados comparten muchos caracteres con el linaje de los osos de las cavernas (Moullé, 1992; Moullé et al., 2006). En 2001 se erige la especie *Ursus dolinensis* García y Arsuaga, 2001 en base a los restos extraídos del yacimiento de la Gran Dolina TD4/5 (ca. 0.8 Ma; García y Arsuaga, 2001). En opinión de los anteriores autores, los fósiles de Gran Dolina presentan una serie de caracteres compartidos con los osos pardos (*Ursus arctos* Linnaeus, 1758) y el linaje de los osos de las cavernas (*Ursus deningeri-Ursus spelaeus* Rosenmüller, 1794), ahora bien, *U. dolinensis* se situaría como especie ancestral del linaje de *U. spelaeus*. Simultáneamente al anterior trabajo, se publica también en 2001 un trabajo sobre los úrsidos del yacimiento alemán de Untermassfeld (ca. 1.0; OIS31; Musil, 2001). En este trabajo también se erige una nueva especie, *Ursus rodei* Musil, 2001. Según el autor, estos restos presentan muchas

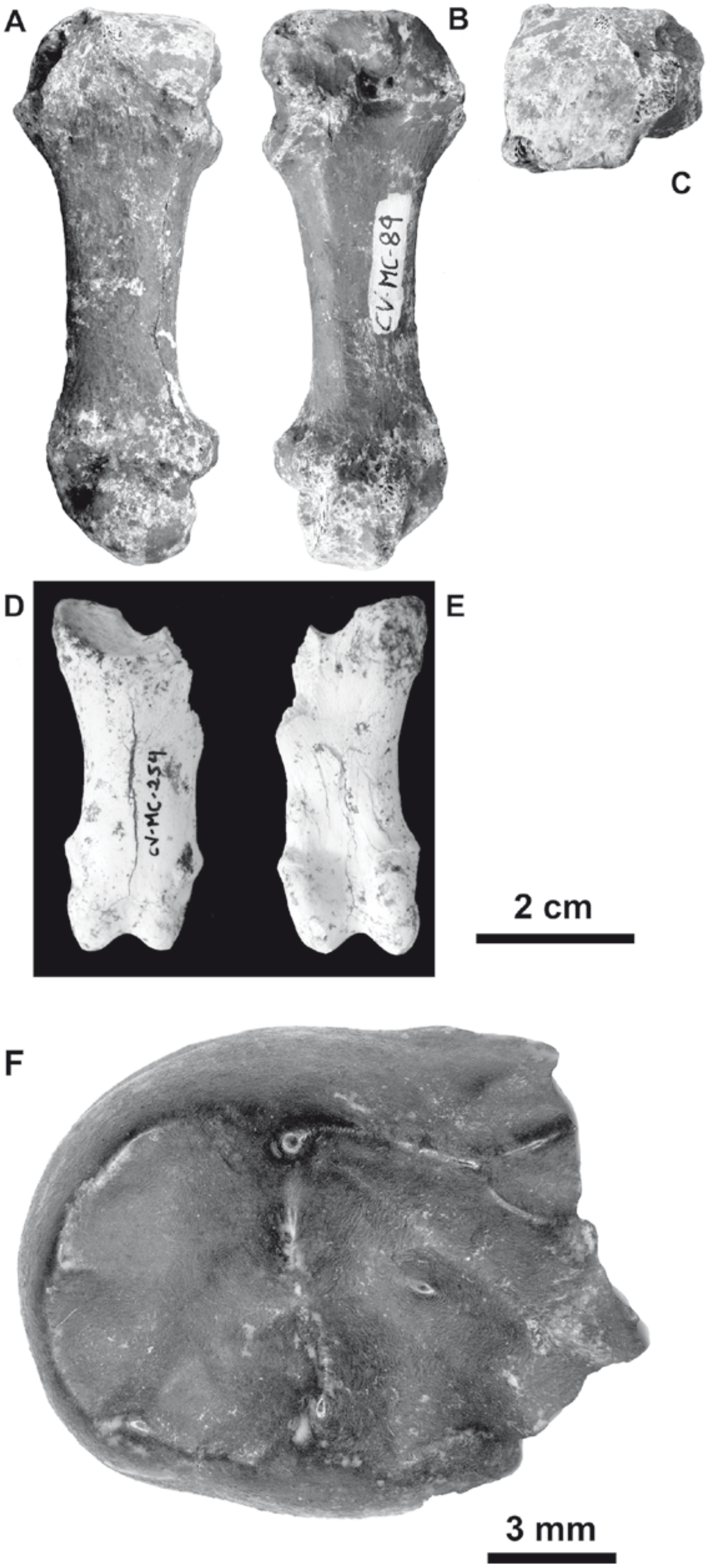

Fig. 1. Elementos postcraneales de *Ursus deningeri* de Cueva Victoria. A-C, primer metatarso izquierdo (MC(CV-MC-89)) en A, vista dorsal; B, vista plantar; C, vista proximal. D-E, falange proximal (MC(CV-MC-254)) en D, vista dorsal; E, vista palmar/plantar. F, fragmento de trigónido de m2 inferior derecho (MC(CV-MC-105)) en vista oclusal.

similitudes morfológicas con *Ursus etruscus* y notables diferencias con *U. deningeri,* siendo su morfología claramente arctoide (Musil, 2001).

La posición filogenética de *U. rodei*, *U. dolinensis* y del úrsido de Vallonnet varía ostensiblemente según la opinión de diversos autores, que los sitúan alternativamente en el linaje arctoide o espeleoide (Petronio et al. 2003; Argant, 2006; Olive, 2006; Kahlke, 2006; Moullé et al., 2006; Petrucci y Sardella, 2009; Petrucci et al, 2013). En 2009 se publican los restos de úrsido del yacimiento de Cal Guardiola en la Cuenca del Vallès-Penedès (Madurell-Malapeira et al., 2009). Estos restos, procedentes del nivel CGRD6 (ca. 0.8 Ma; OIS21), presentan una serie de características claramente espeleoides, compartidas con los osos de Vallonnet, siendo interpretados como una forma arcaica de *U. deningeri*.

En 2010, se publican los restos de úrsidos del yacimiento austríaco de Deutsch-Altenburg (ca. 1.4 Ma; Rabeder et al., 2010), incluyendo los restos del citado yacimiento así como los restos de Ceyssaguet, Süssenborn, Untermassfeld y Gran Dolina en la subespecie *Ursus arctos sussenbornensis* Soergel, 1926 (Rabeder et al., 2010). Según los anteriores autores la morfología de los metacarpianos y metatarsianos de Deutsch-Altenburg tienen claras afinidades con el linaje de los osos pardos.

Finalmente, en un trabajo reciente (Madurell-Malapeira et al., 2014) donde se exponen los datos preliminares sobre los restos de úrsidos de los niveles EVT7 (0.83 Ma; OIS21) y EVT10 (1.0 Ma; OIS31) del yacimiento de Vallparadís Estació (Cuenca del Vallès-Penedès) se concluye que muy probablemente *U. etruscus, U. deningeri* y *U. spelaeus* conforman un único linaje y que todos los úrsidos del Pleistoceno inferior Europeo pertenecen a la línea espeleoide, siendo esta opinión compartida por otros autores (Kurtén, 1968; Petronio et al., 2003). *U. arctos* muy probablemente sería una especie de origen asiático que aparece por primera vez en Europa a inicios del Pleistoceno medio en el yacimiento francés de la Caune de l'Aragó (Moigne et al., 2006).

En los trabajos previos sobre la fauna de Cueva Victoria se cita alternativamente la presencia de *U. etruscus* o *Ursus* sp., pero los restos en los que se basan estas identificaciones nunca han sido descritos (Tabla 1).

Dentición: El único resto dental de Cueva Victoria (MC(-CV-MC-105) consiste en un fragmento mesial de m2. Esta pieza presenta un metacónido tricuspidado con una cúspide central y dos accesorias, mesial y distal, de menor tamaño. Esta morfología es habitual en los úrsidos del Pleistoceno inferior final, siendo identificada en el material de Vallonnet (Moullé, 1992), Gran Dolina TD4/5 (García, 2003) y Untermassfeld (Musil, 2001). Los especímenes de *U. deningeri* y *U. spelaeus* del Pleistoceno medio y superior presentan habitualmente metacónidos triples con cúspides de igual tamaño o incluso cuádruples (Torres, 1984; García, 2003). *U. etruscus* es muy constante en este carácter, presentando siempre un metacónido doble (Torres, 1984; García, 2003). El protocónido de nuestro espécimen, igual que en todos los osos pleistocénicos, es simple (Torres, 1984).

La morfología de este resto sugiere que la forma de Cueva Victoria corresponde a una forma arcaica de *U. deningeri* similar a las registradas en otros yacimientos del mismo período como Untermassfled, Vallonnet, Cal Guardiola CGRD6 o Gran Dolina TD4/5.

Restos postcraneales: Los restos postcraneales de úrsido de Cueva Victoria consisten en un primer metatarsiano completo y una falange proximal con la epífisis proximal rota (respectivamente, MC(CV-MC-89) y MC(CV-MC-254)). La curvatura dorso-palmar del primer metatarsiano es prácticamente inexistente, siendo bastante acentuada en *U. deningeri*, *U. spelaeus* y en menor medida en *U. arctos* y *U. etruscus* (Torres, 1984). En cambio, la morfología de la epífisis proximal claramente convexa antero-posteriormente se asemeja al linaje espeleoide y no a *U. etruscus* y *U. arctos* (Torres, 1984). Las medidas biométricas del primer metatarsiano son diferentes de la especie *U. etruscus* (Tabla 2), siendo nuestro espécimen más largo en dirección proximo-distal (67.8 mm) que los especímenes de Pirro Nord (media de 56.4 (n=3); Petrucci et al., 2013) y con una diáfisis trasversalmente más robusta (14.1 mm; Tabla 2) que los mismos especímenes de Pirro Nord (media de 9.9 (n=3); Petrucci et al., 2013). Los valores biométricos de nuestro espécimen exceden también la variabilidad de *U. deningeri* acercándose a los máximos descritos para *U. spelaeus* y *U. arctos* (Torres, 1984; García, 2003). La misma situación, pero en menor medida, se repite para las variables biométricas de la primera falange de úrsido de Cueva Victoria (Tabla

2; Torres, 1984; García, 2003; Petrucci et al., 2013). Lamentablemente el material postcraneal de los úrsidos del Pleistoceno final descrito en la bibliografía es poco abundante, lo que dificulta la comparación con el existente de Cueva Victoria. Afortunadamente en la colección inédita del yacimiento de Vallparadís Estació y en concreto del nivel EVT10 (ca. 1.0; OIS31; Madurell-Malapeira et al., 2010a) existe un primer metatarsiano inédito EVT25514 con unas dimensiones biométricas y una morfología parecidas al material de Cueva Victoria (Longitud próximo-distal máxima, 66.1 mm y diámetro transversal en la diáfisis, 13.2 mm). La misma situación se repite con varias falanges inéditas del mismo nivel de Vallparadís Estació (EVT23792a; EVT23792b) con unas dimensiones muy similares al espécimen de Cueva Victoria (J.M.-M. observ. person.).

La morfología y dimensiones biométricas del escaso material postcraneal de *Ursus* de Cueva Victoria difiere de la especie *U. etruscus*, asemejándose morfológicamente a *U.deningeri* y *U. spelaeus* aunque con unas dimensiones diferentes. Morfológica y biométricamente, los restos de Cueva Victoria tienen muchas similitudes con el material inédito procedente del nivel EVT10 del yacimiento de Vallparadís Estació con una cronología de 1.0 Ma (Madurell-Malapeira et al., 2010a). El material de Vallparadís Estació y del vecino yacimiento de Cal Guardiola han sido interpretados como una forma arcaica de *U. deningeri* (Madurell-Malapeira et al., 2009; 2014). El material de Cueva Victoria con una cronología cercana a los yacimientos de la Sección de Vallparadís corresponde igualmente a una forma arcaica de *U. deningeri*.

FAMILIA HYAENIDAE Gray, 1869
GÉNERO *Pachycrocuta* Kretzoi, 1937
ESPECIE ***Pachycrocuta brevirostris* (Gervais, 1850)**

Material:

Dentición superior: MC(CV-MC-255), C1 izquierdo; MC(CV-MC-1109), fragmento de corona de C1 derecho; MC(CV-MC-1107), I2 derecho; MC(CV-P-302), fragmento distal de P2 derecho; IMEDEA-C25a, germen de P3 derecho; IMEDEA-C25b, germen de P4 derecho parcial con parastilo, paracono y metacono; IMEDEA-C10, P4 izquierdo completo; IMEDEA-C25c, germen de M1 derecho; MC(CV-P-375), fragmento de corona de dC1 derecho; MC(CV-P-34), fragmento de corona de dC1 izquierdo; MC(CV-SB-14), fragmento de corona de dC1 derecho; MC(CV-BL2-232), dP2 derecho; IMEDEA-C18a, dP2 izquierdo; IMEDEA-C27a, dP2 izquierdo parcial.

Mandíbula y dentición inferior: MC(CV-MC-72), fragmento de corpus mandibular derecho con i2 y alveolo de i3 y c1; IMEDEA-C12(VIC.1a.61), fragmento de corpus mandibular izquierdo con p3 y m1 completos y raíz de p4; MC(CV-MC-73), fragmento de corpus mandibular derecho con alvéolos de m1 y p4; MC(-CV-MC-256), fragmento de corpus mandibular izquierdo con m1 y alveolo distal de p4; MC(CV-MC-138), fragmento de corona de c1 izquierdo; IMEDEA-C25d, germen de i2 derecho; IMEDEA-C25e, germen parcial de i3 derecho; IMEDEA-C25f, germen parcial de c1 derecho; IMEDEA-C18b, germen parcial de p2 derecho; IMEDEA-C27b, p2 derecho parcial; IMEDEA-C25g, germen de p2 derecho; IMEDEA-C25h, germen parcial de p3 derecho; MC(CV-Mc-110), p2 izquierdo parcial; IMEDEA-C11a, p3 izquierdo; IMEDEA-C11b, p4 izquierdo; IMEDEA-C24, p4 derecho; MC(CV-MC-1101), p4 izquierdo; IMEDEA-C25i; germen de p4 derecho; IMEDEA-C25j, germen de m1 derecho; MC(CV-MC-151), fragmento distal de m1 izquierdo; MC(CV-MC-141), dc1 izquierdo; MC(CV-D-63), dp2 derecho; IMEDEA-C18c, dp2 izquierdo; IMEDEA-C18d, fragmento mesial de dp3 izquierdo; IMEDEA-C18e, fragmento mesial de dp3 derecho; MC(CV-SU-69), dp3 izquierdo; IMEDEA-C18f, dp4 derecho; MC(CV-MC-102), dp4 derecho completo; MC(CV-MC-1104), dp4 izquierdo parcial; MC(CV-BL-201), dp4 izquierdo; MC(CV-MC-160), fragmento de premolar inferior; MC(CV-MC-1105), fragmento de corona de canino indeterminado;

Restos postcraneales: IMEDEA-C40a, Tercer metacarpiano derecho sin epífisis distal; IMEDEA-C39a, Tercera falange; MC(CV-D-59), Tercera falange.

Medidas: Tablas 2, 3 y 4.

Descripción:

Dentición superior: **P2:** Premolar de dimensiones mesiodistalmente reducidas en relación al resto de la serie superior. Presenta una cúspide accesoria mesial moderadamente desarrollada y una cúspide accesoria distal bien desarrollada e individualizada del protocono. **P3:** Protocono alto, labio-lingualmente muy desarrolla-

		C1		P3		P4						M1	
Nºinventario	Lat.	L	W	L	W	L	W	Lpr	Lpa	Lp	Lm	L	W
MC(CV-MC-255)	Izq.	20.1	16.1										
IMEDEA-C25a	Der.			23.0	15.3								
IMEDEA-C10	Izq.					41.3	25.2	10.2	13.5	13.2	15.9		
IMEDEA-C25b	Der.					41.7			11.3	14.2	16.3		
IMEDEA-C25c	Der.											6.5	14.0

		dI3		dP2	
Nºinventario	Lat.	L	W	L	W
MC(CV-P-335)	Der.	9.6	6.6		
MC(CV-P-34)	Izq.	9.3	7.1		
MC(CV-SB-14)	Der.	9.4	6.6		
IMEDEA-C18a	Izq.			15.8	9.1
MC(CV-BL2-232)	Der.			15.3	9.1

Tabla 3. Medidas de la dentición superior de *Pachycrocuta brevirostris* de Cueva Victoria.
Abreviaturas: L, longitud mesio-distal; W, anchura labio-lingual; Lpr, longitud mesio-distal del protocono; Lpa, longitud mesio-distal del parastilo; Lp, longitud mesio-distal del paracono; Lm, longitud mesio-distal del metacono.

		p2		p3		p4		m1				
Nº inventario	Lat.	L	W	L	W	L	W	L	W	Lpa	Lpr	Lt
MC(CV-MC-1110)	Izq.	18.8	13.3									
IMEDEA-C25g	Der.	17.5	11.0									
MC(CV-P-25)	Der.			25.0	18.8							
IMEDEA-C11a	Izq.			24.3	18.9							
IMEDEA-C12	Izq.			24.6	19.1			30.1	16.3	15.5	11.0	4.6
MC(CV-MC-1101)	Izq.					26.6	18.2					
MC(CV-MC-114)	Der.						16.7					
IMEDEA-C11b	Izq.					28.7	18.8					
IMEDEA-C24	Der.					27.8	19.7					
IMEDEA-C25i	Der.					25.5	16.0					
MC(CV-MC-256)	Izq.							30.0	15.8	16.7	10.0	4.8
IMEDEA-C25j	Der.							30.1	14.5	13.5	11.7	5.4

		dc1		dp2		dp3		dp4					
Nº inventario	Lat.	L	W	L	W	L	W	L	W	Lpa	Lpr	Ltr	Lta
MC(CV-MC-141)	Izq.	8.8	6.1										
IMEDEA-C18c	Izq.			18.7	9.9								
MC(CV-SU-69)	Izq.					17.9	8.5						
MC(CV-BL-201)	Izq.							21.0	8.7	7.8	8.7	16.6	4.0
MC(CV-MC-102)	Der.							18.5	7.9	6.7	7.7	14.7	3.8
IMEDEA-C18f	Der.							23.1	9.2	8.3	9.1	17.6	5.1

Tabla 4. Medidas de la dentición inferior de *Pachycrocuta brevirostris* de Cueva Victoria.
Abreviaturas: L, longitud mesio-distal; W, anchura labio-lingual; Lpa, longitud mesio-distal del paraconido; Lpr, longitud mesio-distal del protoconido; Ltr, longitud mesio-distal del trigónido; Lta, longitud mesio-distal del talónido.

do, mostrando una pequeña cresta que discurre hasta la cúspide accesoria mesial. La cúspide accesoria distal es de dimensiones reducidas, está bien desarrollada en sentido labio-lingual y se encuentra separada del protocono por una endidura. En general las cúspides accesorias se encuentran menos desarrolladas que en el P2. **P4:** Premolar de grandes dimensiones, con el protocono proyectado en sentido mesio-lingual, diagonalmente al parastilo. El parastilo es de desarrollo moderado y en él se pueden apreciar dos pequeñas crestas que discurren hacia la cara mesial. El paracono, la cúspide de mas entidad del P4, muestra dos aristas asimétricas dirigidas hacia el parastilo y metacono respectivamente (Fig. 2A-C). El metastilo, la cúspide más baja pero de mayor recorrido mesio-distal, acaba distalmente en un pequeño cíngulo labial. **M1:** Molar muy reducido en relación a la serie premolar. Muestra tres cúspides diferenciadas. El metacono se encuentra reducido y en una posición intermedia entre lingual y labial, donde se situan respectivamente protocono y paracono de dimensiones parecidas.

Dentición decidual superior: **dP2:** Premolar alargado en sentido mesio-distal y sin aparente compresión labio-lingual. Protocono alto con una cúspide accesoria distal de perfil bajo pero bien desarrolada labio-lingualmente, presencia de un pequeño cingulo lingual. La parte mesial del protocono presenta una cresta fina que se extiende hacia el margen mesial (Fig. 3J-L).

Dentición inferior: **p2:** Protocónido alto con dos cúspides accesorias, mesial y distal, bien diferenciadas. La cúspide accesoria mesial se emplaza mesiolingualmente mientras que la distal, de mayor entidad, se encuentra en el vértice labio-distal (Fig. 2I-K). **p3:** Premolar comprimido en sentido mesio-distal y bien desarrollado en sentido labio-lingual. Presenta protocónido muy desarrollado y ancho labio-lingualmente, con una cúspide accesoria mesial muy reducida, casi ausente (Fig. 2F-H). La cúspide accesoria distal se encuentra comprimida mesio-distalmente y tiene muy poca altura en relación al protocónido. **p4:** Premolar con una ligera compresión mesio-distal. Protocónido muy desarrollado con dos cúspides accesorias, mesial y distal, muy grandes (Fig. 2O-Q). La cúspide mesial tiene poca altura en relación a la distal y está separada del protocónido por una hendidura. La cúspide accesoria distal, presenta la longitud mesio-distal menor que el protocónido y está comprimida mesio-distalmente, mientras que lingualmente presenta un pequeño cíngulo. **m1**: Molar con dos cúspides principales, el protocónido y el paracónido (Fig. 2R-T). La cúspide anterior, el paracónido, muestra mayor desarrollo mesio-distal y altura que la posterior, el protocónido, poseyendo este último una longitud mesio-distal equivalente a 2/3 del paracónido. Se puede observar un pequeño metacónido, muy reducido, en el margen distolingual del protocónido. El talónido, bien desarrollado, tiene dos cúspides de pequeña entidad (hipocónido e hipoconúlido).

Dentición decidual inferior: **dp2:** Premolar deciduo con el extremo distal más ancho labio-lingualmente que el mesial. Protocónido bajo, con una ligera cresta que se extiende desde el protocónido hasta la región mesio-lingual. No se distingue cúspide accesoria mesial (Fig. 3M-O). La cúspide accesoria distal está presente pero poco desarrollada y separada del protocónido por una pequeña depresión (Fig. 3M-O). **dp3:** Procotónido alto, esbelto y bien desarrollado mesio-distalmente. La cúspide accesoria mesial es más baja y de dimensiones más reducidas que la distal, presentando esta última un pequeño cíngulo distal (Fig. 3P-R). **dp4:** Protocónido y paracónido de la misma longitud mesio-distal, siendo el protocónido más alto. Además, el protocónido presenta un pequeño cíngulo basal en el vértice mesio-labial. El talónido de talla diferente en las tres piezas estudiadas presenta siempre dos cúspides, entocónido e hipoconúlido (Fig. 3A-I).

Esqueleto postcraneal: Tres elementos del esqueleto postcraneal de *P. brevirostris* han podido ser identificados; un tercer metacarpiano que no conserva la epífisis distal y dos falanges distales (respectivamente, IMEDEA-C40a; IMEDEA-C39a; MC(CV-O-59)). El tercer metacarpiano posee la diáfisis sub-circular, completamente recta y muy robusta. En la epífisis proximal, la faceta para la articulación del magno es fuertemente convexa, prolongándose hacia la parte posterior. En la cara medial, la faceta para la articulación del segundo metacarpiano esta localizada en posición antero-medial siendo de pequeñas dimensiones, forma rectangular y alargada en sentido antero-posterior. En vista lateral la faceta articular para el cuarto metacarpiano se sitúa en posición anterior, es de morfología rectangular y convexa en sentido próximo-distal. Las dos falanges distales identificadas muestran afinidades con los hiénidos modernos en cuanto a la morfología de la faceta articular proximal, muy cóncava y una prolongación muy

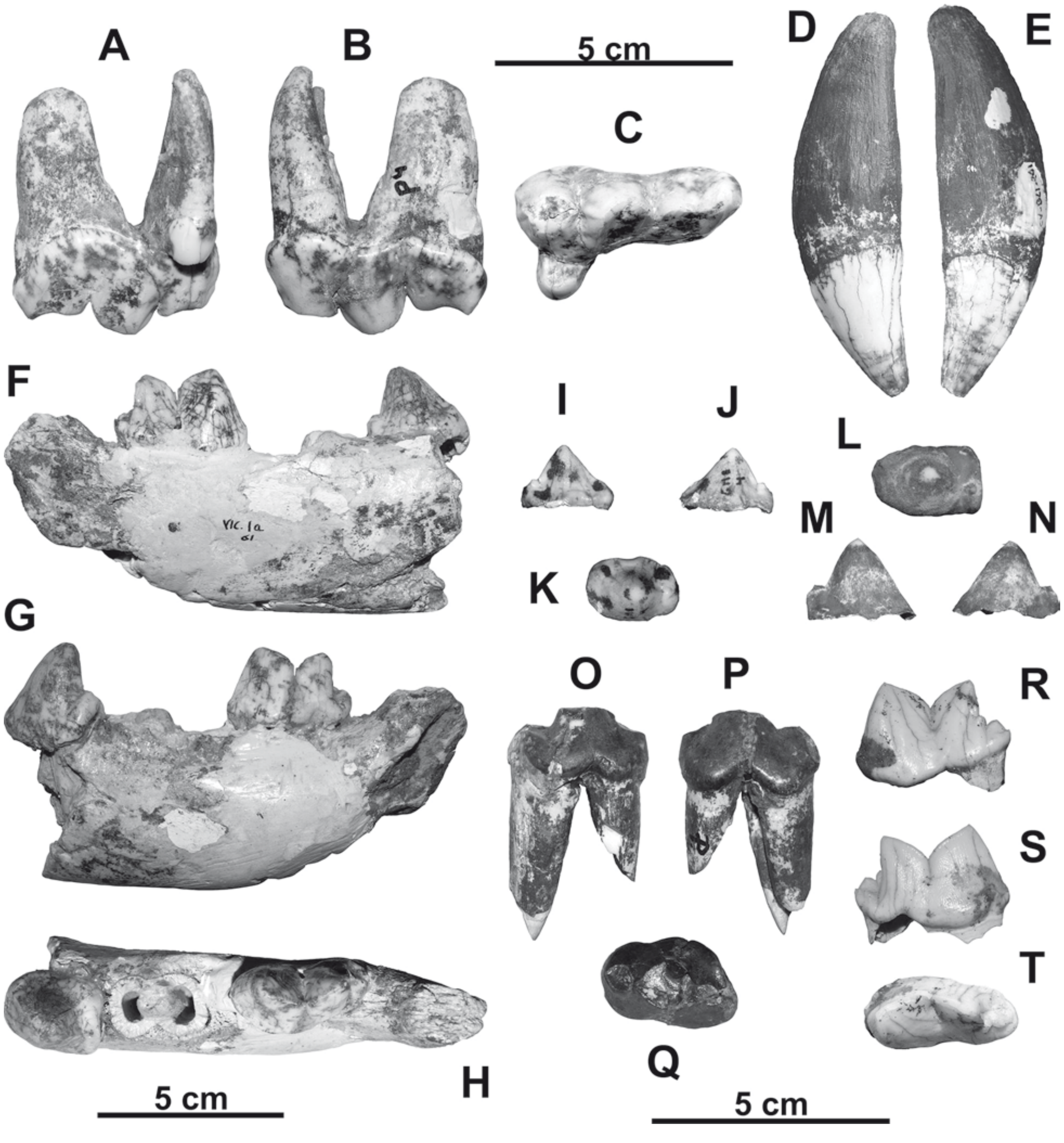

Fig. 2. Dentición definitiva de *Pachycrocuta brevirostris* de Cueva Victoria. A-C, P4 izquierdo (IMEDEA-C10) en A, vista lingual; B, vista labial; C, vista oclusal. D-E, C1 izquierdo (MC(CV-MC-255)) en D, vista labial; E, vista lingual. F-H, corpus mandibular (IMEDEA-C12) con p3 y m1 en F, vista lingual; G, vista labial; H, vista oclusal. I-K, p2 izquierdo (MC(CV-GNB-4)) en I, vista lingual; J, vista labial; K, vista oclusal. L-N, p3 izquierdo (MC(CV-MC-97)) en L, vista oclusal; M, vista lingual; N, vista labial. O-Q, p4 izquierdo (IMEDEA-C11b) en O, vista lingual; P, vista labial; Q, vista oclusal. R-T, m1 derecho (IMEDEA-C25c) en R, vista lingual; S, vista labial; T, vista oclusal.

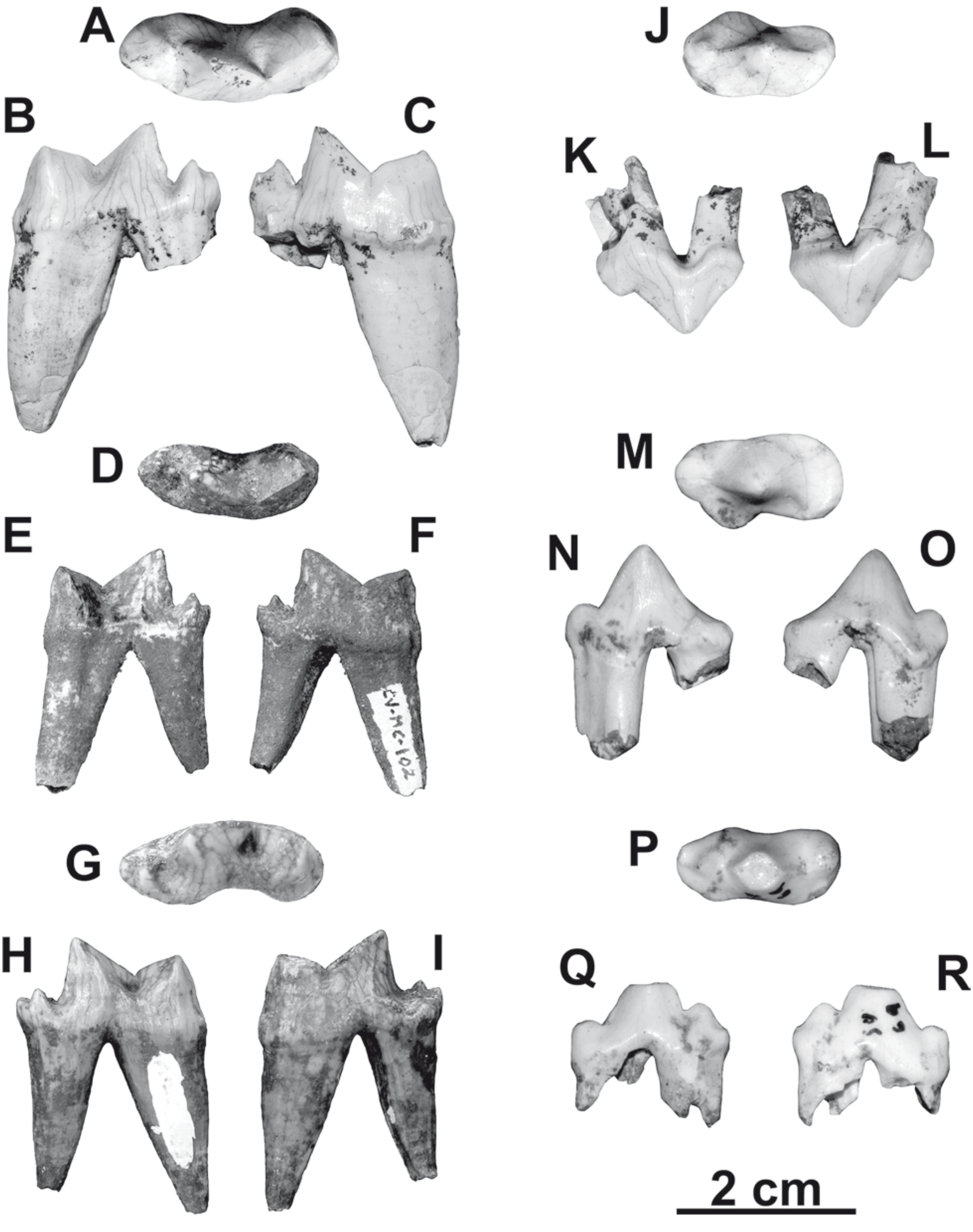

Fig. 3. Dentición decidual de *Pachycrocuta brevirostris* de Cueva Victoria. A-C, dp4 derecho (IMEDEA-C18f) en A, vista oclusal; B, vista lingual; C, vista labial. D-F, dp4 derecho (MC(CV-MC-102)) en D, vista oclusal; E, vista lingual; F, vista labial. G-I, dp4 izquierdo (MC(CV-BLI-201)) en G, vista oclusal; H, vista lingual; I, vista labial. J-L, dP2 izquierdo (IMEDEA-C18a) en J, vista oclusal; K, vista lingual; L, vista labial. M-O, dp2 izquierdo (IMEDEA-C18c) en M, vista oclusal; N, vista lingual; O, vista labial. P-R, dp3 izquierdo (MC(CV-SU-69)) en P, vista oclusal; Q, vista lingual; R, vista labial.

acentuada y comprimida lateralmente de la parte distal (García, 2003). Las dos falanges distales presentan dimensiones biométricas muy diferentes debido a que probablemente IMEDEA-C39a corresponde a una falange de un dedo central y MC(CV-O-59) a una falange de un dedo lateral.

Discusión:

Antecedentes: *P. brevirostris* se dispersa en Europa en el límite Villafranquiense medio-superior (1.8-2.0 Ma) siendo registrada por primera vez en los yacimientos de Olivola (Italia) y Fonelas P-1 (España) (Palombo et al., 2008; Arribas y Garrido, 2008). Desde su llegada al continente, *P. brevirostris* es una especie muy bien documentada, gracias al gran número de restos dentales de los yacimientos del Pleistoceno inferior final (Palombo et al., 2008; Palmqvist et al., 2011). Las acumulaciones óseas, probablemente originadas por este hiénido de más de 110 kg de peso, han sido documentadas en numerosos yacimientos, siendo uno de ellos el de Venta Micena, en la Cuenca de Guadix-Baza (Palmqvist et al., 2011). El último registro de esta especie en Europa corresponde al nivel EVT7 del yacimiento de Vallparadís Estació (ca. 0.83 Ma; Madurell-Malapeira et al., 2010a).

Ya desde los primeros trabajos sobre los carnívoros de Cueva Victoria (Pons-Moyà y Moyà-Solà, 1978) se cita sin discusión la presencia de *P. brevirostris* en el yacimiento, probablemente debido a las grandes dimensiones y robustez de los fragmentos de corpus mandibulares y premolares encontrados (Pons-Moyà y Moyà-Solà, 1978; Tabla 1)

Dentición: La presencia de un talónido alargado en el m1, las cúspides accesorias mesiales y distales en los premolares 2 y 3 (tanto superiores como inferiores), así como la anchura labio-lingual de los mismos y la presencia de M1 tricuspidado descartan la atribución de los restos al género *Crocuta* Kaup 1828. La especie *C. crocuta* es registrada por primera vez en Europa el nivel TDW4 de la Gran Dolina de Atapuerca (ca. 0.8 Ma; García, 2003), siendo a partir de este momento un elemento muy habitual en las asociaciones de carnívoros del Pleistoceno medio y superior Europeo. Si bien, esta especie se encuentra localizada fuera de África en el Corredor Levantino en 'Ubeidiya, Israel, en una cronología de 1,2-1,5 Ma (Ballesio, 1986; Martínez-Navarro et al., 2009).

La comparación realizada del material disponible de Cueva Victoria con el de otros yacimientos Europeos como Venta Micena, Cal Guardiola CGRD2, Untermassfeld, Vallonnet o Upper Valdarno (Moullé, 1992; Turner y Antón, 1996; Turner, 2001; Madurell-Malapeira et al., 2009; Palmqvist et al., 2011), muestra que tanto morfológicamente como biométricamente, y salvo una pequeña variabilidad de tamaño los especímenes con dentición adulta, es muy similar en todos los ellos. La mayor variabilidad morfológica observada se encuentra localizada en el m1, con cambios en: a) el numero de cúspides presentes en el talónido (1-2); b) la presencia/ausencia del metacónido; c) la altura del paracónido y protocónido. También cabe destacar una pequeña variabilidad en el P4 en cuanto a la longitud del parastilo en relación con el paracono. Por último, la presencia de abundante material deciduo, así como los gérmenes dentales, dan peso a la teoría de que el yacimiento fue un cubil de hienas (Gibert et al., 1992; Gibert, 1999).

Esqueleto postcraneal: El registro de la especie *P. brevirostris* en Europa, aunque numeroso, consiste básicamente en elementos dentales aislados y fragmentos mandibulares, siendo probablemente la colección del yacimiento alemán de Untermassfeld la más numerosa, con un mínimo de 11 individuos identificados (Turner, 2001). En cualquier caso el numero de restos postcraneales publicados de esta especie es muy reducido siendo probablemente la colección del yacimiento chino de Zoukoudian-1 la que presenta más abundancia de elementos postcraneales (Pei, 1934). Lamentablemente, en las anteriores publicaciones no consta ningún tercer metacarpiano ni terceras falanges descritas. La asignación de estos elementos a *P. brevirostris* se debe a las similitudes de estos elementos con los correspondientes a las formas tanto modernas como extintas del género *Crocuta* (García, 2003; Testu, 2006).

FAMILIA FELIDAE Gray, 1821
GÉNERO *Homotherium* Fabrini, 1890
ESPECIE ***Homotherium latidens*** **(Owen, 1846)**

Material: IMEDEA-C34, I1 izquierdo; IMEDEA-C41a, fragmento apical de C1 derecho; IMEDEA-C15, c1 izquierdo; MC(BI-33), c1 derecho; IMEDEA-C40b, segundo metatarsiano derecho.

Medidas: Tabla 2, 5 y 6.

Descripción:

Dentición superior: **I1:** Presenta una corona alta de morfología triangular con dos tubérculos, uno localizado en el lado medial y el otro en el distal. Los dos tubérculos poseen crenulaciones en su cara lingual y están unidos por un marcado cíngulo (Fig. 4E-G). La raíz es larga y comprimida en sentido mesio-distal (Fig. 4F). **C1**: El fragmento apical de C1 identificado (IMEDEA-C41a) muestra la compresión mesio-distal y las crenulaciones en ambas aristas típicas del género *Homotherium* (Fig. 4H-I).

Dentición inferior: **c1***:* De los dos c1 identificados, MC(CV-02-276) se encuentra muy mal conservado, probablemente debido a meteorización química. El segundo, IMEDEA-C40b, se encuentra en perfecto estado, mostrando raíz y corona muy comprimidas en sentido mesio-distal (Fig. 4A-B). En vista mesial, presenta dos aristas claras (una labial y otra lingual) donde se pueden apreciar las crenulaciones típicas del género *Homotherium*. En la cara labial, la arista termina en la base en un pequeño tubérculo de reducidas dimensiones.

Esqueleto postcraneal: El segundo metatarsiano se encuentra bien conservado aunque la parte posterior de la epífisis proximal está rota. (Fig. 4M-Q). La epífisis proximal posee una faceta de articulación con el mesocuneiforme de morfología triangular y ligeramente cóncava. En vista lateral, la epífisis proximal presenta dos facetas, una anterior y otra posterior, de morfología sub-circular para la articulación del tercer metatarsiano. La diáfisis es rectilínea con morfologíaa aplanada en vista lateral.

Discusión:

Antecedentes: El género *Homotherium* es registrado por primera vez en Europa a inicios del Villafranquiense (MN16; ca. 3.0 Ma), aunque su distribución biogeográfica también incluye África, Asia y América. Este género es muy común en las asociaciones de carnívoros Villafranchienses europeas hasta la transición Pleistoceno inferior-medio, cuando muy probablemente la dispersión de *Panthera leo* (Linnaeus 1758) desde África implicó una dura competencia para estas formas (Palombo et al., 2008; Madurell-Malapeira, 2010). Las últimas citas de *Homotherium* en Europa corresponden probablemente a las localidades de Fontana Ranuccio y Gran Dolina TD10 alrededor de los 0.4 Ma (Gliozzi et al., 1997; García, 2003). Algunos autores, en cambio, defienden una extinción europea de *Homotherium* mucho más tardía, siendo esta hipótesis respaldada por la reciente localización de una hemi-mandíbula de este género en el Mar del Norte con una cronología aproximada de 28.000 años (Reumer et al., 2003).

La asignación específica de los restos de *Homotherium* europeos ha sido foco de controversia los últimos cincuenta años. Diferentes especies han sido propuestas: *H. latidens* Owen, 1846; *H. crenatidens* Fabrini, 1890; *H. sainzelli* Aymard, 1853; *H. nestianus* Fabrini, 1890; o *H. moravicum* Woldrich, 1917. En opinión de Kurtén (1968), ciertas diferencias morfológicas en los caninos superiores de este género respaldarían la creación de dos cronoespecies: *H. crenatidens* para los restos del Pleistoceno inferior *y H. latidens* para los del Pleistoceno medio. En cambio Turner (1999) basándose en el gran dimorfismo sexual presente en estas formas y su extensa variabilidad interespecífica argumenta que las diferencias propuestas por Kurtén (1968) pueden no ser válidas y agrupa todas las formas europeas en la especie *H. latidens* que tiene prioridad respecto a *H. crenatidens*. La hipótesis expuesta por Turner (1999) ha ganado mucho peso en los últimos años después de la descripción de la numerosa colección de restos de esta forma procedentes del yacimiento de Incarcal (Galobart et al., 2003), donde se ha podido documentar la variabilidad interespecífica y dimorfismo ya apuntados por Turner (1999).

La primera referencia a la presencia de *Homotherium* en Cueva Victoria corresponde a un trabajo de Gibert y colaboradores (1988) donde se cita la presencia de este género pero sin descripción alguna. En todos los trabajos posteriores se cita igualmente la presencia de *Homotherium* pero el material no ha sido nunca descrito (Tabla 1).

Dentición: La morfología de la dentición extraída del yacimiento de Cueva Victoria, por la presencia de tubérculos bien desarrollados y de un cíngulo lingual en los incisivos; la crenulación de las aristas y el grado de compresión mesio-distal de los caninos tanto inferiores como superiores, respalda la inclusión de este material en la especie *H. latidens*. La comparación del material estudiado con la excelente colección del yacimiento de Incarcal (Galobart et al., 2003b) tanto a nivel morfológi-

			I1		I3		C1		P3		P4					
Especie	Nºinventario	Lat.	L	W	L	W	L	W	L	W	L	W	Lpr	Lpa	Lp	Lm
H. latidens	IMEDEA-C34	Izq.	10.4	10.4												
Megantereon sp.	MC (CV-Mc-1108)	Der.							14.1	6.5						
P. gombaszoegensis	MC(CV-MC-135)	Der.			8.0	8.1										
P. gombaszoegensis	MC(CV-MC-64)	Izq.			8.4	9.1										
P. gombaszoegensis	IPS43363	Der.									30.1	16.9	11.6	7.8	11.9	11.9
P. gombaszoegensis	MC (CV-MC-103)	Der.							20.6	10.8						
P. gombaszoegensis	MC(CV-MC-1102)	Izq.							20.4	10.4						
L. pardinus	IPS43408	Izq.					8.0	6.3								
L. pardinus	MC (CV-SMI-25)	Der.					10.5	7.0								
L. pardinus	MC (CV-2011-260)	Izq.					8.4	6.9								
L. pardinus	MC (CV-P-36)	Der.							10.6	5.1						
L. pardinus	IPS43366	Der.									18.1	9.1	4.1	4.3	8.9	7.0
L. pardinus	IPS43231	Der.								5.1	16.1	8.2	4.4	3.7	7.0	6.9
L. pardinus	MC (CV-P-303)	Der.									16.8			3.5	7.6	6.7
L. pardinus	IMEDEA-41b	Der.													6.5	6.7

Tabla 5. Medidas de la dentición superior de las diferentes especies de félidos registradas en Cueva Victoria.
Abreviaturas: L, longitud mesio-distal; W, anchura labio-lingual; Lpr, longitud mesio-distal del protocono; Lpa, longitud mesio-distal del parastilo: Lp, longitud mesio-distal del paracono; Lm, longitud mesio-distal del metacono.

			c1		p3		p4		m1										
Especie	Nºinventario	Lat.	L	W	L	W	L	W	L	W	Lp	Lpr	Ld	Lm	Lsd	Hp4	Hm1	Hd	Hr
H. latidens	IMEDEA-C15	Izq.	14.7	10.3															
H. latidens	MC (CV-BI-33)	Der.	13.7	10.7															
P. gombaszoegensis	MC (CV-MC-61)	Izq.			15.6	7.4	19.8	10.6					18.0						
P. gombaszoegensis	MC (CV-MC-191)	Izq.			14.4	7.0													
P. gombaszoegensis	IMEDEA-C14a	Izq.					21.6	10.2	21.0	11.8	11.1	14.6				37.3	35.0		
P. gombaszoegensis	IMEDEA-C14b	Der.					19.7	10.7								39.8			
P. gombaszoegensis	IPS43183	Der.							20.1	10.7	10.8	12.9							
P. gombaszoegensis	IMEDEA-C38	Izq.							20.3	10.8	9.4	13.1							
P. pardoides	IPS46144	Der.	13.0	9.1	12.6	6.3	16.7	8.71	18.6	8.9	10.7	9.7	9.9		45.5	25.2	23	24.6	
P. pardoides	IPS46145	Izq.			12.5	6.8													
P. pardoides	MC (CV-MC-63)	Der.	13.7	10.6															
L. pardinus	IMEDEA-C9	Der.			8.3	4.1	12.4	5.3	13.2	5.7	6.4	7.7	10.8	97.2	32.4	18.4	16.6	16.4	39.8
L. pardinus	MC (CV-MC-115)	Izq.			8.5	4.6	10.6	5.3	12.9	5.8	6.8	8.0	9.6	86.8	32.9	16.5	15.6	14.8	38.0
L. pardinus	MC (CV-MC-253)	Izq.			9.3	4.6							10.6					19.3	
L. pardinus	IMEDEA-C4	Izq.							14.6	5.7	7.4	8.9	5.7		33.4	15.5	14.5	15.3	
L. pardinus	MC (CV-MC-1103)	Der.							13.1	5.8	5.4	6.4							

Tabla 6. Medidas de la dentición y mandíbula de las diferentes especies de félidos registradas en Cueva Victoria.
Abreviaturas: L, longitud mesio-distal; W, anchura labio-lingual; Lp, longitud mesio-distal paraconido; Lpr, longitud mesdio-distal protoconido; Ld, longitud de la diastema; Lm, longitud mandibular; Lsd, longitud de la serie dental; Hpa, altura del corpus mandibular debajo del p4; Hm1, altura del corpus mandibular debajo del m1; Hd, altura del corpus mandibular al nivel de la diastema; Hr, altura del ramus.

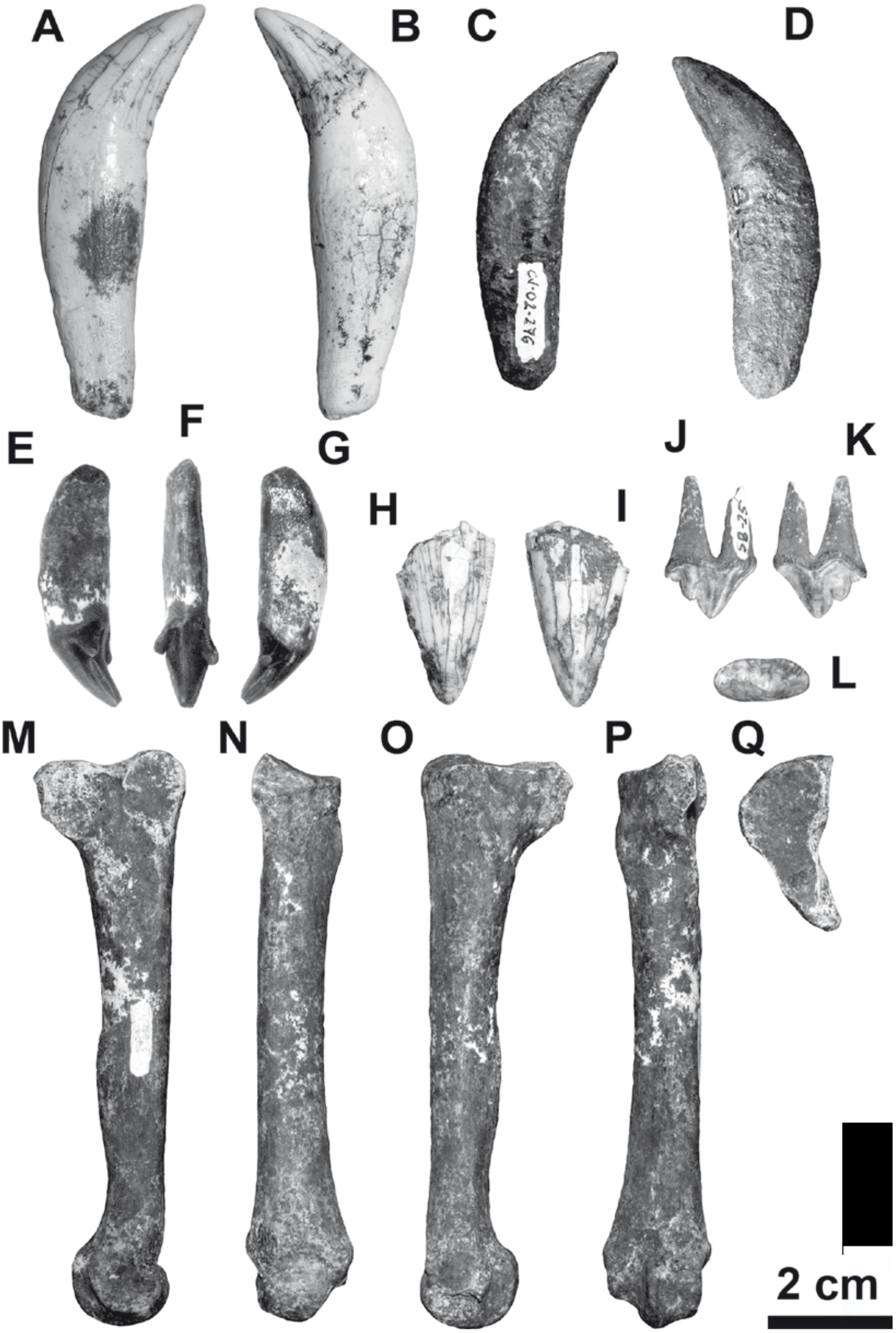

Fig. 4. Restos craneales y postcraneales de *Homotherium latidens* y *Megantereon* sp. de Cueva Victoria. A-B, c1 izquierdo de *H. latidens* (IMEDEA-C15) en A, vista labial; B, vista lingual. C-D, c1 derecho de *H. latidens* (MC(CV-BI-33) en C, vista lingual; D, vista bucal. E-F, I1 izquierdo de *H. latidens* (IMEDEA-C34) en E, vista distal; F, vista lingual; G, vista mesial. H-I, C1 derecho de *H. latidens* (IMEDEA-C41a) en H, vista labial; I, vista lingual. J-L, P3 derecho de *Megantereon* sp. (MC(CV-MC-1108)) en J, vista labial; K, vista lingual; L, vista oclusal. M-Q, segundo metatarsiano derecho de *H. latidens* (IMEDEA-C40b) en M, vista lateral; N, vista dorsal; O, vista medial; P, vista plantar; Q, vista proximal.

co como biométrico respalda igualmente la asignación (Tablas 5 y 6).

Esqueleto postcraneal: El segundo metatarsiano derecho (IMEDEA-C40b) de Cueva Victoria posee las mismas características morfológicas y biométricas que el mismo elemento recuperado del yacimiento de Incarcal-V, IN-V-15 (Galobart et al., 2003b) (Tabla 2). Estos elementos y otros restos recuperados de los yacimientos de Incarcal son próximo-distalmente más cortos y más esbeltos que el material del yacimiento francés de Senèze (Ballesio, 1963), este hecho sustentaría la idea de una gran variabilidad interespecífica en esta especie (Galobart et al., 2003b).

GÉNERO *Megantereon* Croizet and Jobert, 1828
ESPECIE ***Megantereon* sp.**

Material: MC(CV-MC-1108), P3 derecho.

Medidas: Tabla 5.

Descripción: Premolar muy comprimido labio-lingualmente con dos raíces. Posee un paracono alto y muy comprimido. Parastilo ausente pero metastilo bien desarrollado y comprimido lateralmente. Disto-lingualmente se puede apreciar un cíngulo bien marcado que envuelve el metastilo en su parte distal.

Discusión:

Antecedentes: El género *Megantereon* ha sido identificado básicamente a partir de restos dentales aislados y fragmentos mandibulares en Europa, America del Norte, Asia y África. En Europa, las citas más tempranas de estas formas se remontan a inicios del Villafranquiense en el yacimiento francés de Les Etouaires (ca. 3.5 Ma; Sardella, 1998). A partir de inicios del Villafranquiense, *Megantereon* es una forma ampliamente registrada en Europa sobre todo en el yacimiento francés de Senèze donde se recuperó un esqueleto muy completo recientemente descrito (Christiansen y Adolfssen, 2007). La desaparición de *Megantereon* de las asociaciones Villafranquienses se sitúa cronológicamente alrededor del millón de años siendo las últimas citas conocidas los yacimientos de Untermassfeld y el nivel EVT10 de Vallparadís Estació (Hemmer, 2001; Madurell-Malapeira et al., 2010a).

Al igual que en el caso del género *Homotherium*, la taxonomía del género *Megantereon* ha sido foco de polémica en los últimos veinte años. Numerosas especies han sido descritas tanto en Europa como en Asia y África: *M. cultridens* (Bravard, 1828); *M. megantereon* (Bravard, 1828); *M. whitei* Broom, 1827; *M. nihowaensis* Teilhard de Chardin y Piveteau, 1930; *M. falconeri* Pomel, 1853; *M. sivalensis* Falconer y Cautley, 1868 o *M. ekidoit* Werdelin y Lewis, 2000. Las primeras revisiones efectuadas del género apuntaban a la existencia de una única especie *M. cultridens* (Turner, 1987; Turner y Antón, 1997) poco conocida debido a la escasez de restos, variación geográfica y a un gran dimorfismo sexual. Los últimos trabajos en cambio, apoyan la existencia de dos especies: *M. cultridens* y *M. whitei* (Martínez-Navarro y Palmqvist, 1995, 1996; Palmqvist et al., 2007). Según esta interpretación, *M. cultridens* representaría la especie primitiva registrada en América y Eurasia hasta la base del Villafranquiense superior, mientras que *M. whitei* sería una especie de origen africano, más derivada, que agruparía todas las formas plio-pleistocénicas africanas y del Villafranquiense superior euroasiático.

En el primero trabajo sobre la fauna de Cueva Victoria (Pons-Moyà y Moyà-Solà, 1978), se indica la existencia de una forma atribuible a un Machairodóntido en base a una raíz de canino superior, apuntándose que podría corresponder al género *Megantereon*. Esta asignación tentativa fue corroborada en un trabajo posterior (Carbonell et al., 1981), donde se asigna el resto a *Megantereon* sp. En los trabajos posteriores se hace referencia a la presencia de *Megantereon* sp. o *M. cultridens* sin describir más restos o justificar la asignación (Tabla 1). En las colecciones estudiadas no se ha podido localizar este resto pero si el P3 descrito anteriormente.

Dentición: La variabilidad morfológica y biométrica de los P3 del género *Megantereon* ha sido evidenciada por diversos autores (Viret, 1954; Ficarelli, 1979; Turner, 1987; Qiu et al., 2004; Christiansen y Adolfssen, 2007; Palmqvist et al., 2007). En general, esta pieza está mucho menos reducida que en los géneros *Homotherium* y *Smilodon*, siendo un premolar muy comprimido labio-lingualmente con dos raíces, paracono de altura variable, presencia de metastilo bien diferenciado y cíngulo linguo-distal. En algunas formas como las de Senèze o Saint-Vallier también se observa la presencia de un pequeño parastilo. En general, las formas derivadas adscritas a *M. whitei* simplifican el número de cúspides, estando ausente el parastilo, y evidencian una mayor compresión labio-lingual. Ahora bien, los numerosos especímenes del yacimiento chino de Longdan (ca. 2.0 Ma; Qiu et al., 2004), adscritos a *M. cultridens* por Palmqvist et al. (2007) presentan compresión labio-lingual acentuada, ausencia de parastilo y reducción ligera del metastilo. La morfología y las dimensiones biométricas del P3 (MC(CV-SB-25)) de Cueva Victoria permiten adscribirlo al género *Megantereon,* pero la gran variabilidad morfológica observada y la escasez de restos nos hacen ser cautos con la asignación específica, con lo que se prefiere dejar la asignación a nivel genérico.

GÉNERO *Panthera* Oken, 1816
ESPECIE ***Panthera gombaszoegensis*** **Kretzoi, 1938**

Material: MC(CV-MC-64), I3 izquierdo; MC(-CV-MC-135), I3 derecho, MC(CV-MC-103), P3 derecho; MC(CV-MC-1102), P3 izquierdo; IPS43363, P4 derecho; IMEDEA-C14a, fragmento de corpus izquierdo con p4 y m1; IMEDEA-C14b, fragmento de corpus derecho con p4 y alveolo de p3; MC(CV-MC-61), fragmento de corpus izquierdo con p3 y p4; MC(CV-MC-191), p3 izquierdo; IPS43183, m1 derecho; IMEDEA-C38, m1 izquierdo; MC(CV-MC-177), fragmento distal de dp3 izquierdo; MC(CV-MC-163), fragmento distal de dp3 izquierdo; IPS43420, navicular izquierdo; IMEDEA-39b; Falange proximal del dedo I izquierdo; IPS43404, falange medial izquierda.

Medidas: Tablas 2, 5 y 6.

Descripción:

Dentición superior: **I3:** Incisivos de corona baja y raíz comprimida mesio-distalmente, presentan cíngulo lingual bien marcado. **P3:** Premolares con el paracono muy desarrollado en dirección labio-lingual y simétrico en vista lateral. Parastilo bien desarrollado y de morfología circular en el extremo mesio-lingual del diente. Metastilo presente, pero poco diferenciado de la arista distal del paracono. Cíngulo distal bien desarrollado (Fig. 6 D-I). **P4:** Protocono de reducidas dimensiones y orientado en sentido labio-lingual. Parastilo reducido en sentido mesio-distal y más bajo que paracono y metastilo. Paracono comprimido labio-lingualmente y más alto que el metastilo. Metastilo comprimido labio-lingualmente y con poco desarrollo mesio-distal (Fig. 6A-C).

Dentición inferior: **p3:** Premolar con protocónido triangular y simétrico en vista lateral, en el que se pueden observar dos cúspides accesorias, siendo la mesio-lingual (paracónido) de más entidad que la distal y de morfología sub-circular (Fig. 5A-C; Fig.6 T-V). **p4:** Premolares con un protocónido muy desarrollado y ligeramente inclinado hacia la región distal. La cúspide accesoria anterior (paracónido) está bien definida siendo de mayores dimensiones que la distal que posee un pequeño cíngulo distal (Fig. 5). **m1:** Molar con el paracónido mesio-distalmente más corto y bajo que el protocónido. No se observan ni cíngulos ni talónido (Fig.5 D-I; Fig. 6N-S).

Esqueleto postcraneal: Tres elementos del esqueleto postcraneal han podido ser identificados como pertenecientes a *P. gombaszoegensis*. El navicular IPS43420, muestra en vista proximal una faceta astragalar sub-circular, ligeramente cóncava y proyectada hacia la zona postero-proximal. La faceta calcaneal se encuentra en el extremo latero-posterior, es de reducidas dimensiones y con contorno sub-circular. En vista distal se pueden apreciar dos facetas, una sub-circular en el extremo anterior de grandes dimensiones para la articulación del ectocuneiforme, y una segunda, sub-rectangular, muy reducida en el extremo postero-lateral para la articulación del mesocuneiforme. La falange proximal del dedo I izquierdo (IMEDEA-39b), muestra una diáfisis corta y muy robusta. La epífisis proximal posee una faceta de articulación muy inclinada hacia la región distal (Fig. 6J-K). La falange medial izquierda (IPS43404) muestra la diáfisis corta y robusta, ligeramente convexa en sentido proximal (Fig.6L-M).

Discusión:

Antecedentes: Formas de félidos de gran tamaño y filogenéticamente relacionadas con el jaguar americano *Panthera onca* (Linnaeus, 1758), han sido identificadas en diferentes yacimientos europeos del Villafranchiense y Galeriense, así como en numerosos yacimientos americanos. La aparición de estas formas en Europa corresponde al subcron paleomagnético Olduvai (ca. 2.0 Ma; Ficcarelli y Torre, 1968; Hemmer et al., 2010) y los últimos registros corresponden al comienzo del Pleistoceno medio (ca. 0.5-0.4 Ma; O'Regan y Turner, 2004; Hemmer et al., 2010).

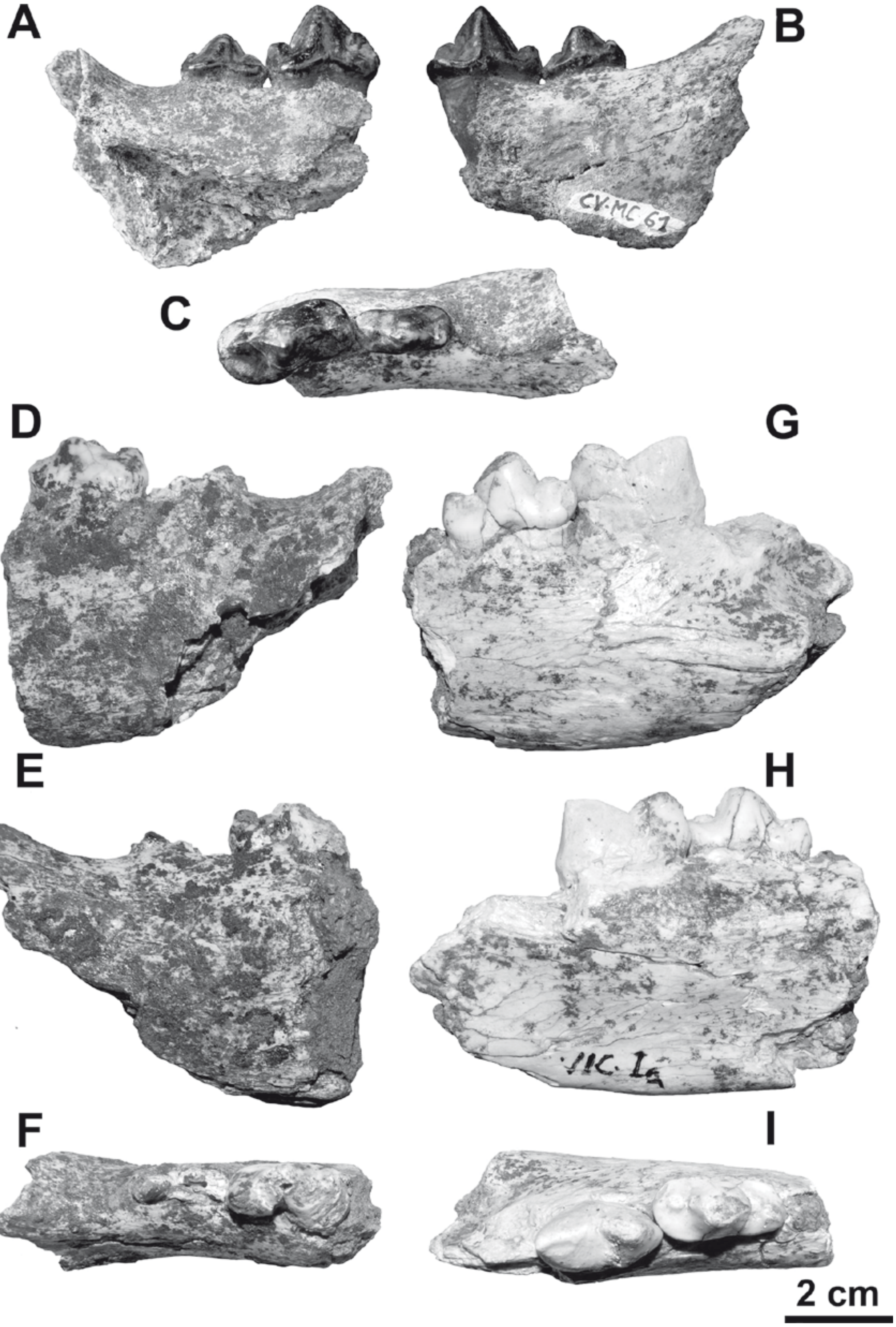

Fig. 5. Restos mandibulares de *Panthera gombaszoegensis* de Cueva Victoria. A-C, fragmento de corpus mandibular izquierdo con p3-p4 (MC(CV-MC-61) en A, vista labial; B, vista lingual; C, vista oclusal. D-F, fragmento de corpus mandibular derecho con p3 (IMEDEA-C14b) en D, vista labial; E, vista lingual; F, vista oclusal. G-I, fragmento de corpus mandibular izquierdo con p4-m1 (IMEDEA-C14a) en G, vista labial; H, vista lingual; I, vista oclusal.

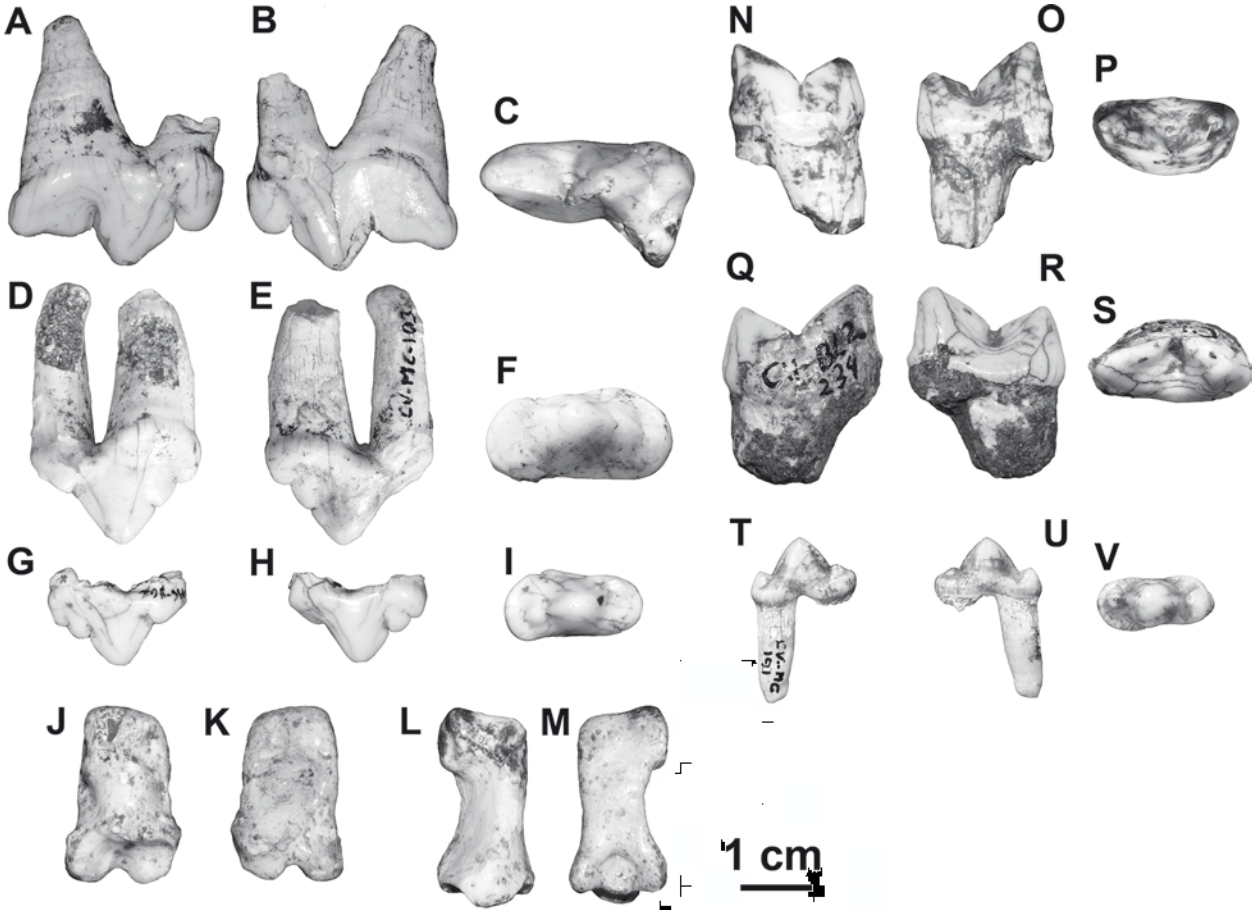

Fig. 6. Restos dentales y postcraneales de *Panthera gombaszoegensis* de Cueva Victoria. A-C, P4 derecho (IPS43363) en A, vista labial; B, vista lingual; C, vista oclusal. D-F, P3 derecho (MC(CV-MC-103) en D, vista labial; E, vista lingual; F, vista oclusal. G-I, P3 izquierdo (MC(CV-MC-1102) en G, vista labial; H, vista lingual; I, vista oclusal. J-K, falange proximal del dedo I izquierdo (IMEDEA-C39b) en J, vista anterior; K, vista posterior. L-M, falange medial izquierda (IPS43404) en L, vista dorsal; M, vista palmar/plantar. N-P, m1 derecho (IPS43183) en N, vista labial; O, vista lingual; P, vista oclusal. Q-S, m1 izquierdo (IMEDEA-C38) en Q, vista labial; R, vista lingual; S, vista oclusal. T-V, p3 izquierdo (MC(CV-MC-191) en T, vista labial; U, vista lingual; V, vista oclusal.

Los jaguares europeos han sido incluidos dentro de diferentes especies o subespecies, aunque preferentemente en *P. gombaszoegensis* o *P. toscana* (Schaub, 1949) (Hemmer, 2001; Olive, 2006; Von Koenigswald et al., 2006; Argant et al., 2007). O'Regan y Turner (2004), en una revisión exhaustiva del material del yacimiento holandés de Tegelen, sugieren que todos los jaguares europeos pertenecen a una sola especie con una gran variabilidad intrerespecífica y un marcado dimorfismo sexual, asignando los restos a la especie *P. gombaszoegensis*. En una revisión reciente de Hemmer y colaboradores (2010), los autores exponen que muy probablemente las formas europeas y americanas del Pleistoceno son simplemente subespecies de *P. onca*. Siguiendo esta hipótesis, las formas del Villafranquiense Europeo (*P. onca toscana*) y asiático (*P. onca georgica*) serian las especies ancestrales de las formas americanas (*P. onca augusta*) y del Galeriense Europeo (*P. onca gombaszoegensis*).

En el primer trabajo sobre los carnívoros de Cueva Victoria Pons-Moyà y Moyà-Solà (1978) ya citan la presencia en el yacimiento de la especie *Felis* aff. *toscana* a partir de un fragmento de mandíbula (Fig. 5G-I). En las siguientes publicaciones ya se incluye este material en la especie *P. gombaszoegensis* (Tabla 1) aunque la mayoría del material atribuible a esta especie nunca ha sido descrito ni figurado (Fig. 5-6).

Dentición superior: Los restos de dentición superior de *P. gombaszoegensis* no son muy habituales en los yacimientos del Pleistoceno inferior europeo. El único material disponible ha sido obtenido de los yacimientos del Upper Valdarno y Olivola (Italia; Ficcarelli y Torre, 1968), Gerakarou (Grecia; Koufos, 1992), Untermassfeld (Alemania; Hemmer, 2001) y Trinchera Dolina (España, García, 2003) aunque también se cito la presencia de un P3 en el yacimiento de Galería (España, Morales et al., 1987) que posteriormente ha sido identificado como un p3 de *Panthera leo* (García, 2003). La morfología y dimensiones de los P3 estudiados presentan muchas similitudes con el material de los yacimientos mencionados, con la presencia de paracono alto y desarrollado, así como cíngulo distal robusto. Hay cierta variabilidad en la ausencia/presencia del parastilo mesio-lingual, presente en el material de Cueva Victoria, Untermassfeld y Upper Valdarno y ausente en el de Gerakarou. Igualmente, la robustez e individualización de la cúspide accesoria posterior, bien desarrollada y claramente separada del paracono en el material de Gerakarou, Untermassfeld, Upper Valdarno y Olivola, está menos marcado en el de Cueva Victoria. Referente al P4 (IPS43363) las características observadas son las descritas para esta especie con un protocono robusto y perpendicular al parastilo, ausencia de ectoparastilo y presencia de metastilo afilado y moderadamente alargado en sentido mesio-distal (Koufos, 1992). Sólo se ha podido observar cierta variabilidad en la longitud mesio-distal del parastilo en referencia al paracono/metastilo, siendo el parastilo reducido en el material de Cueva Victoria y bien desarrollado en las piezas de Untermassfeld (Hemmer, 2001).

Dentición inferior: A diferencia del caso anterior, el registro de dentición inferior y mandíbulas de *P. gombaszoegensis* es bastante abundante en Europa, en yacimientos como Upper Valdarno y Olivola (Italia, Ficcarelli y Torre, 1968); Vallonnet y Chateau (Francia; Moullé, 1992; Argant, 1991), Tegelen (Holanda; O'Regan y Turner, 2004), Untermassfeld (Alemania; Hemmer, 2001) y Akhalkalaki y Dmanisi (Georgia; Hemmer et al., 2001, 2010) entre otros. La morfología del p3 es muy constante en toda la muestra disponible, con protoconido bajo y con dos cúspides accesorias, una mesial y otra distal, presentes, siendo la mesial normalmente de morfología circular y algo más grande que la distal (O'Regan y Turner, 2004). Ahora bien, las dimensiones y anchura labio-lingual de los especímenes varia, siendo los especímenes con edad mas antigua algo más anchos labio-lingualmente (Hemmer et al., 2010, Fig. 2B). Los dos p3 estudiados, de longitud mesio-distal reducida y comprimidos labio-lingualmente, poseen dimensiones similares a las observadas en los especímenes del Pleistoceno inferior terminal (Tabla 5; Hemmer et al., 2010). En lo referente a los p4, la morfología es también muy constante, con una cúspide accesoria anterior grande y bien diferenciada, y una cúspide accesoria posterior grande pero baja, con un cíngulo distal bien desarrollado. Igual que en el caso de los p3, los p4 de inicios del Villafranchiense final (Olivola, Upper Valdarno, Tegelen) suelen ser más anchos labio-lingualmente que el material posterior (Untermassfeld, Chateau, Vallonnet), y el material de Cueva Victoria, al igual que los especimenes de los estos yacimientos, presenta el p4 comprimido labio-lingualmente (Tabla 5, Hemmer et al., 2010). De la misma manera que en los casos anteriores, la morfología de los m1 descritos en la bibliografía muestran una gran constancia, con paracónido mesio-distalmente más corto y bajo que el protocónido. Si bien, en algunos casos, sobretodo en las formas del Pleistoceno inferior tardío y del Pleistoceno medio, se puede observar una pequeña protuberancia lingual entre el paracónido y el protocónido. Esta protuberancia no está presente en el material de Cueva Victoria. En cuanto a las comparaciones biométricas, el material de Cueva Victoria se sitúa en los limites inferiores del rango de variabilidad de la especie (Fig. 3D de Hemmer et al., 2010), estando probablemente causada esta alta variabilidad por el marcado dimorfismo sexual presente en la especie.

Esqueleto postcraneal: El escaso material postcraneal conocido de *P. gombaszoegensis* procede de los yacimientos Untermassfled y Château (Argant, 1991; Hemmer, 2001). En la colección de Chateau están citados un navicular y varias segundas falanges, aunque en ninguna de las dos colecciones se ha recuperado ninguna falange proximal del primer dedo. El material procedente de Château tiene muchas similitudes con el de Cueva Victoria, ya que el navicular muestra el mismo grado de curvatura en la faceta astragalar y la misma posición de la faceta calcanear. A su vez, las segundas falanges también muestran una diáfisis corta, robusta y ligeramente curvada (Argant, 1991; Fig. 24). No se ha podido comparar la falange proximal del primer dedo con ningún resto de *P. gombaszoegensis,* pero presenta muchas similitudes tanto morfológicas como biométricas con el material actual de *P. onca*, con una diáfisis corta y robusta y una faceta proximal muy inclinada hacia la zona distal.

GÉNERO *Puma* Jardine, 1834
ESPECIE ***Puma pardoides* (Owen, 1846)**

Material: IPS46144, corpus mandibular derecho con c1, p3, p4 y m1; IPS46145, p3 izquierdo; MC(CV-MC-63), c1 derecho completo.

Medidas: Tabla 6.

Descripción:

Dentición: **p3**: Los dos p3 estudiados muestran parastílido bien desarrollado de morfología circular, que está más desarrollado que la cúspide accesoria distal (Fig. 7A-C). **p4:** muestra una cúspide accesoria mesial bien desarrollada y no comprimida labio-lingualmente. El protocónido es esbelto y asimétrico en vista bucal. La cúspide accesoria distal está ligeramente comprimida en sentido labio-lingual, presentando además un cingúlido distal (Fig. 7A-C). **m1:** robusto con un protocónido ligeramente más largo en sentido mesiodistal y alto en comparación con el paracónido (Fig. 7A-C).

Discusión:

Antecedentes: El registro ibérico de la especie *Puma pardoides* ha sido recientemente revisado por Madurell-Malapeira et al. (2010b), en el que se concluye que esta especie está presente en los yacimientos de La Puebla de Valverde, Cueva Victoria y en el nivel EVT7 del yacimiento de Vallparadís Estació. El material de Cueva Victoria que se describe en el presente estudio ya fue descrito en profundidad en el citado artículo a excepción del c1 derecho (MC(CV-MC-63) que presenta las mismas características morfológicas que IPS46144. Nos remitimos a Madurell-Malapeira et al., (2010b) para las comparaciones morfológicas precisas con otro material de la misma especie de otros yacimientos europeos así como con otras especies actuales de félidos de tamaño similar. Según los datos disponibles, *P. pardoides* se registra en la Península Ibérica desde la MN17 en la Puebla de Valverde, hasta el yacimiento de Vallparadís Estació, con una edad de 0.83 Ma. Posteriormente al citado artículo se ha descrito nuevo material de esta especie procedente del yacimiento gaditano de Sierra del Chaparral, con una cronología aproximada de 0.99-0.78 Ma (Giles-Pacheco et al., 2011). El registro de esta especie en Europa se sitúa en cronologías similares, siendo las primeras citas conocidas correspondientes a la MN16b de Perrier-Étouaires (Hugueney et al., 1989) y Montopoli (ca. 2.6 Ma; Cherin et al., 2013). Igual que en la Península, *P. pardoides* se perpetua en Europa hasta el límite Pleistoceno inferior-medio en localidades como Untermassfeld o Stránská Skála (Hemmer, 2001).

En los trabajos previos, *Viretailurus schaubi* (Viret, 1954). sinónimo de *P. pardoides,* es ya citado en el trabajo de Carbonell et al. (1981) sin que se describan los restos. La mandíbula IPS46144 presumiblemente procede de las excavaciones de Joan Pons-Moyà del año 1977, pues pertenece a su colección personal, y, aunque esta especie está citada en la mayoría de los trabajos posteriores sobre Cueva Victoria (Tabla 1), no ha sido descrita hasta el reciente articulo de Madurell-Malapeira y colaboradores (2010b).

GÉNERO *Lynx* Linnaeus, 1758
ESPECIE ***Lynx pardinus* Temminck, 1827**

Material:

Dentición superior: IPS43408, C1 izquierdo; MC (CV-2011-260), C1 izquierdo; MC(CV-SMI-25), fragmento de C1 derecho; IPS43231, fragmento de maxilar derecho con P4 y fragmento distal de P3; MC(CV-P-36), P3 derecho; IPS43366, P4 derecho; IMEDEA-C41b, fragmento distal de P4 derecho con paracono y metacono; MC(CV-P-303), P4 derecho con protocono fragmentado.

Mandíbula y dentición inferior: IMEDEA-C9, hemimandíbula derecha con p3-m1 y alvéolo de c1; IMEDEA-C4, hemimandíbula izquierda con m1 y alvéolos de c1 a p4; MC(CV-MC-115), hemimandíbula izquierda con p3-m1 y alvéolo de c1; MC(CV-MC-253), fragmento de corpus mandibular izquierdo con p3 y alvéolo de c1; MC(CV-MC-1103), fragmento de corpus mandibular derecho con m1; MC(CV-MC-275), fragmento mesial de dp3 izquierdo.

Restos postcraneales: MC(CV-U-34), fragmento ventral de escápula izquierda; MC(CV-MC-179), fragmento de escápula izquierda; IMEDEA-C40d, epífisis distal de húmero derecho; IMEDEA-C40c, epífisis proximal de radio izquierdo; MC(CV-MC-162), segmento distal de radio izquierdo; MC(CV-D-57), fragmento de epífisis proximal de ulna izquierda; IMEDEA-C32a, quinto metacarpiano izquierdo; IMEDEA-C27c, segmento distal de tibia de-

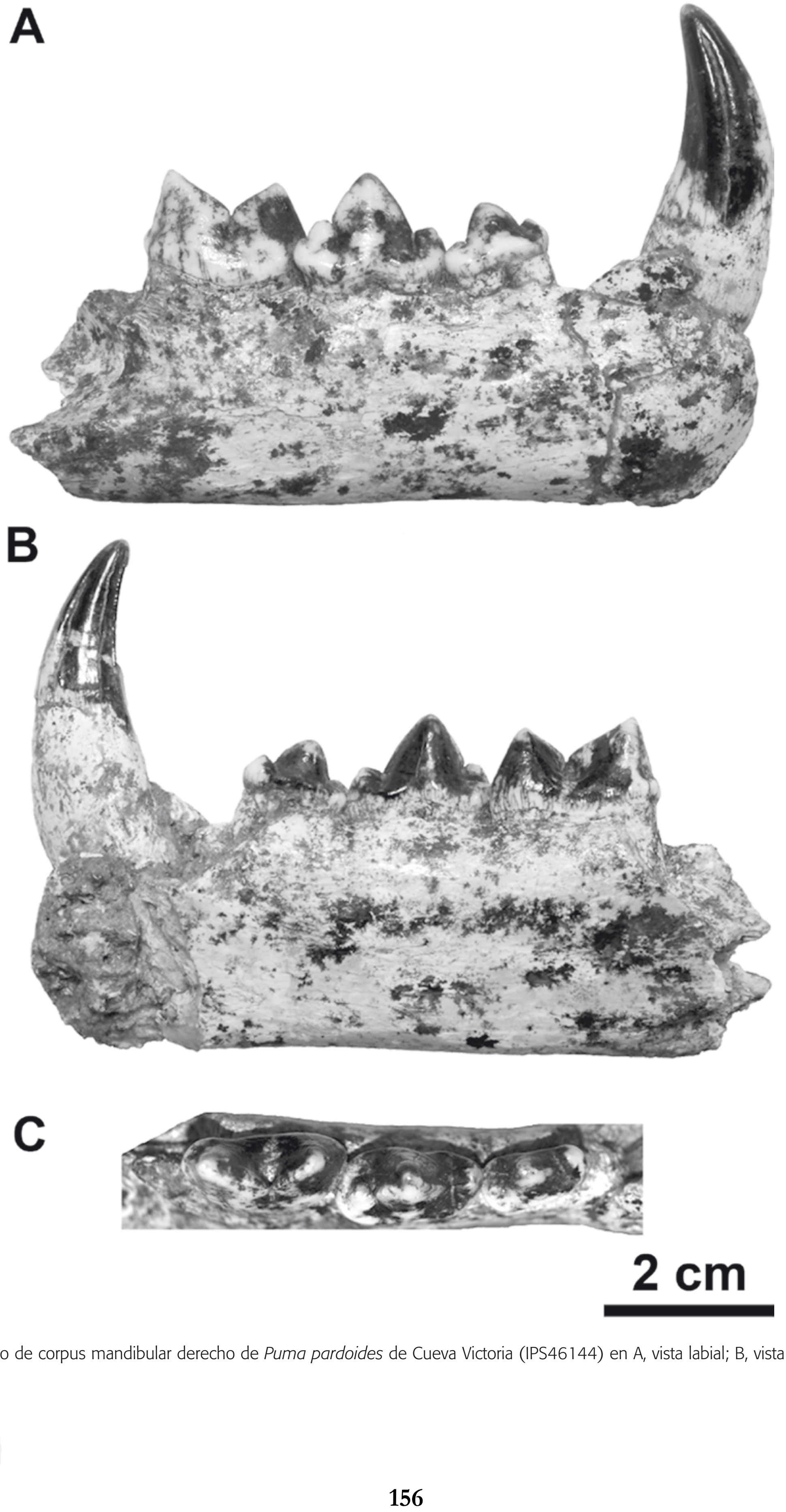

Fig. 7. Fragmento de corpus mandibular derecho de *Puma pardoides* de Cueva Victoria (IPS46144) en A, vista labial; B, vista lingual; C, vista oclusal.

recha; MC(CV-D81), fragmento distal de tibia derecha; MC(CV-MC-132), fragmento de diáfisis de tibia derecha sin epífisis proximal; IMEDEA-C40e, segmento proximal de tercer metatarsiano izquierdo; IMEDEA-C32b, quinto metatarsiano derecho; IMEDEA-C32c, falange proximal izquierda; IMEDEA-C32d, falange proximal derecha; MC(CV-MC-169), falange medial derecha.

Medidas: Tablas 2, 5 y 6.

Descripción:

Dentición superior: **P3**: Premolar comprimido labio-lingualmente, con paracono alto y redondeado. Ausencia de parastilo. Metastilo de reducidas dimensiones y morfología circular. Se observa un pequeño cíngulo distal. **P4:** Protocono emplazado mesio-distalmente de dimensiones reducidas. Parastilo poco comprimido labio-lingualmente y mesio-distalmente muy corto respecto a paracono y metastilo. Presencia de ectoparastilo mesio-bucal en IPS43366 y ausencia en IPS43232 (Fig. 9 A-F) y MC(CV-P-303). Paracono bien desarrollado y muy prominente mesio-distalmente con respecto el metastilo. Metastilo reducido mesio-distalmente con morfología redondeada hacia la región distal (Fig. 9A-F).

Mandíbula: Mandíbula baja y robusta con un diastema corto. Presencia de dos forámenes mentonianos, uno debajo del diastema y otro debajo de la raíz mesial del p3. Fosa masetérica profunda, llegando al nivel de la raíz distal del m1. Rama ascendente y proceso coronoides fuertemente inclinados distalmente. Apófisis angular robusta y dirigida horizontalmente hacia posición distal. Apófisis condilar a la altura de la serie dentaria en vista lateral (Fig. 8A-K).

Dentición inferior: **p3:** Premolar comprimido labio-lingualmente con protocónido alto y simétrico en vista lateral. Paracónido presente y bien desarrollado en IMEDEA-C9 y muy reducido en MC(CV-MC-115). Cúspide accesoria distal de pequeñas dimensiones y morfología circular acompañada por cíngulo distal incipiente (Fig. 8A-K). **p4:** Premolar robusto labio-lingualmente con protocónido alto. El paracónido está bien desarrollado y posee morfología circular. Cúspide accesoria posterior emplazada labio-distalmente y comprimida en sentido labio-lingual acompañada por cíngulo distal incipiente (Fig. 8A-K). **m1:** Protocónido y paracónido de la misma longitud mesio-distal, siendo el protocónido ligeramente más alto. Presencia de una cúspide linguo-distal de muy reducidas dimensiones en MC(CV-MC-115) y ausencia total de ella en IMEDEA-C9, IMEDEA-C4 (Fig. 8A-K) y MC(CV-MC-1103).

Esqueleto postcraneal: Las dos escápulas estudiadas (MC(CV-U-34) y MC(CV-MC-179)) presentan la fosa glenoide de morfología circular, la apófisis coracoides está ligeramente expandida hacia el lado interno (Fig. 9G-H). El fragmento distal de húmero (IMEDEA-C40d) presenta un foramen supracondilar reducido próximo-distalmente. Los epicondilos medial y lateral son reducidos (Fig. 9I-J). La superficie articular está dividida en dos segmentos de dimensiones parecidas, lateral y medial, por una depresión central estrecha y profunda. Los dos fragmentos de radio (IMEDEA-C40c y MC(-CV-MC-162)) presentan una tuberosidad radial alargada en sentido próximo-distal, pudiéndose observar una pequeña tuberosidad palmar, con una pequeña fosa sub-circular en su zona proximal. En la epífisis distal, el proceso estiloide radial está muy prolongado distalmente, presentando en vista anterior las inserciones de los extensores radial y oblicuo muy marcadas (Fig. 9M-N). El quinto metacarpiano (IMEDEA-C32a) muestra la articulación proximal semicircular y fuertemente convexa. La diáfisis es sub-triangular y no presenta torsión (Fig. 9O-P) . Tres fragmentos distales de tibia han sido estudiados (IMEDEA-C27c, MC(CV-MC-132a, MC(-CV-132b), todos presentan la epífisis distal de contorno trapezoidal en vista distal, los maléolos son robustos y bien desarrollados y las facetas articulares distales para el astrágalo són relativamente poco profundas (Fig. 9K-L). El tercer metatarsiano (IMEDEA-C40e) conserva la diáfisis y la epífisis proximal. La faceta proximal para la articulación del ectocuneiforme es ligeramente convexa. Medialmente, las facetas articulares para el segundo metacarpiano están situadas en el vértice anterior y posterior de la epífsis proximal, siendo relativamente reducidas y de morfología sub-rectangular. Lateralmente, las facetas para la articulación de cuarto metacarpiano están situadas igualmente en los vértices anterior y posterior y tienen morfología sub-triangular. El quinto metatarsiano (IMEDEA-C32b) muestra una diáfisis muy esbelta y una ligera torsión dorso-palmar.

Discusión:

Antecedentes: Los linces de finales del Rusciniense y del Villafranchiense han sido habitualmente incluidos a

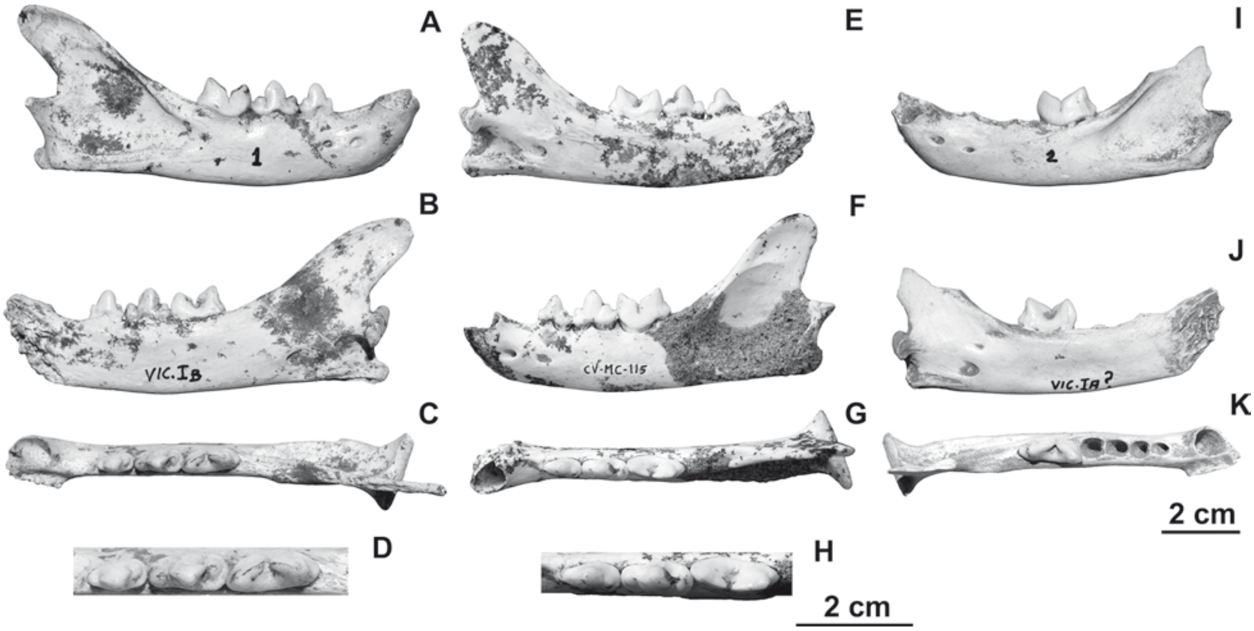

Fig. 8. Hemimandibulas de *Lynx pardinus* de Cueva Victoria. A-D, hemimandíbula derecha con p3-m1 (IMEDEA-C9) en A, vista labial; B, vista lingual; C, vista oclusal; D, detalle de la dentición en vista oclusal. E-H, hemimandibula izquierda con p3-m1 (MC(CV-MC-115) en E, vista lingual; F, vista labial, G, vista oclusal; H, detalle de la dentición en vista oclusal. I-K, hemimandíbula izquierda con m1 (IMEDEA-C4) en I, vista labial; J, vista lingual; K, vista oclusal.

la especie *Lynx issiodorensis* Croizet y Jobert, 1828 que muy probablemente tuvo una distribución Euroasiática durante el Villafranchiense, y que sería la especie ancestral de *L. pardinus* y *L. lynx* (Linnaeus, 1758) (Ficcarelli y Torre, 1977; Werdelin, 1981). *L. pardinus* sería una especie de origen Europea que durante el Pleistoceno medio y superior fue paulatinamente sustituida por el emigrante asiático *L. lynx* hasta quedar restringida a la Península Ibérica. De manera habitual, las formas de lince del Pleistoceno medio y superior han sido adscritas a *Lynx spelaeus* (Boule, 1906) o bien a *L. pardinus spelaeus* (ver discusión en Ficcarelli y Torre, 1977; Werdelin, 1981), aunque varios autores incluyen los linces del Pleistoceno medio y superior de Francia y Italia en la línea filogenética de *L. lynx* y en la especie *L. spelaeus* (Bonifay, 1971; Ficcarelli y Torre, 1977; Testu, 2006). Werdelin (1981), en una extensa revisión de la línea evolutiva de los linces en base a datos biométricos, concluye que *L. issiodorensis* es la especie ancestral de las cuatro especies actuales de lince: *L. pardinus*, *L. lynx*, *L. rufus* (Schreber, 1777) y *L. canadensis* (Kerr, 1792). Werdelin (1981) detecta una progresiva reducción de la talla desde las formas iniciales del Villafranquiense hacia las formas más pequeñas como *L. pardinus*. En opinión del anterior autor, es posible separar en dos subespecies *L. issiodorensis*: una subespecie correspondiente al Villafranquiense inferior y medio *L. issiodorensis issiodorensis*; y una segunda subespecie del Villafranquiense final *L. issiodorensis valdarnensis* que luego continuaría con la línea filogenética *L. pardinus spelaeus* y *L. pardinus* durante el Pleistoceno medio y superior.

En un trabajo posterior de Morales y colaboradores (2003) se describen por primera vez en detalle los materiales de lince del yacimiento de Layna (Soria, MN15), concluyendo que el material de Layna presenta muchas afinidades morfológicas con el actual *Caracal caracal* (Schreber, 1776) aunque con una talla algo mayor. En base a los anteriores datos, los autores erigen una nueva especie para el material de Layna, *Caracal depereti* Morales et al., 2003. En este trabajo también se analizan las características morfológicas y biométricas de los linces del Villafranquiense europeo, concluyendo que debido a la semejanza con del material de Layna, las formas de este período tienen que incluirse en el género *Caracal*, concretamente en la especie *C. issiodorensis*.

Finalmente, en un trabajo reciente Cipullo (2010) estudia la evolución de los linces del Plioceno al Pleistoceno del área mediterránea, descartando los datos propuestos por Morales y colaboradores (2003), y dando por válida la teoría expuesta por Werdelin (1981).

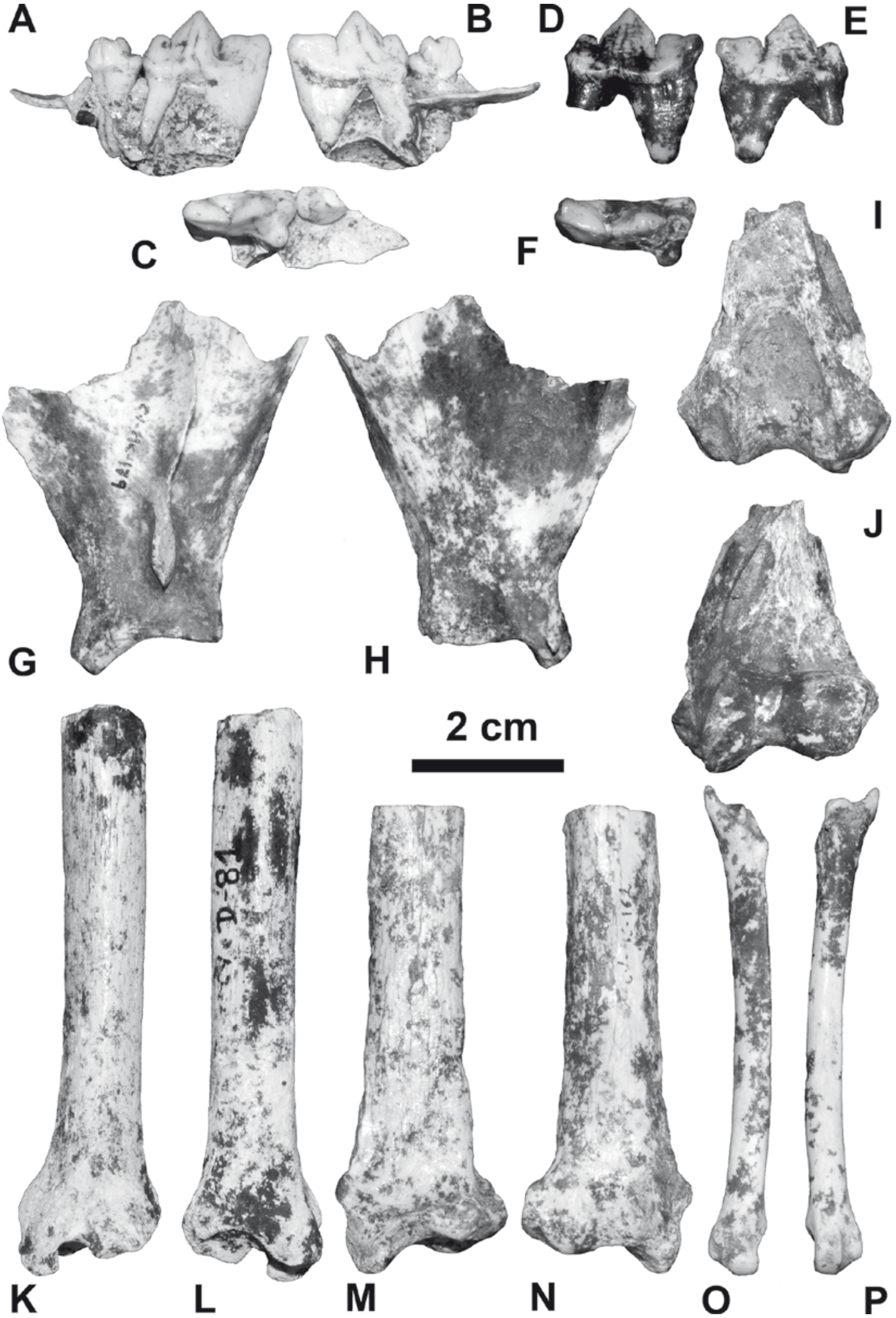

Fig. 9. Dentición superior y restos postcraneales de *Lynx pardinus* de Cueva Victoria. A-C, fragmento de maxilar izquierdo con P3 parcial y P4 (IPS43231) en A, vista labial; B, vista lingual; C, vista oclusal. D-F, P4 derecho (IPS43366) en D, vista labial; E, vista lingual; F, vista oclusal. G-H, escápula izquierda (MC(CV-MC-179)) en G, vista lateral; H, vista medial. I-J, epífisis distal de húmero derecho (IMEDEA-C40d) en I, vista dorsal; J, vista ventral. K-L, segmento distal de tíbia (MC(CV-D81)) en K, vista dorsal; L, vista ventral. M-N, segmento distal de radio izquierdo ((MC(CV-MC-162)) en M, vista dorsal; N, vista ventral. O-P, quinto metatarsiano derecho (IMEDEA-C32b) en O, vista dorsal; P, vista plantar.

Concerniente a Cueva Victoria, desde el primer trabajo de Pons-Moyà y Moyà-Solà (1978) se cita la presencia de *Lynx* en el yacimiento, continuándose la cita en trabajos posteriores (Tabla 1). Pero es el trabajo de Pons-Moyà (1985), donde se describen con detalle los restos de *Lynx* de la acumulación, en el que se concluye que no pertenecen a *L. issiodorensis*, si no a *L. spelaea*, la cual es una forma ya incluida en el linaje del lince ibérico.

Dentición superior: El P3 estudiado tiene el paracono alto, no se observa parastilo y el metastilo es de reducidas dimensiones, con pequeño cíngulo distal. Esta morfología es la habitual en *L. issiodorensis* y *L. pardinus* así como en *Caracal*. Los P4 de Cueva Victoria muestran protocono reducido, así como paracono alto y separado del metastilo por una leve incisión, lo cual es común a *L. issiodorensis*, *L. pardinus* y *Caracal*. La única variante es la presencia de ectostilo en uno de los tres ejemplares estudiados (IPS43366), siendo esta característica apuntada por Kurtén (1978) como típica de *L. issiodorensis*. Los ejemplares de Cueva Victoria, morfológica y biométricamente, se asemejan a las formas del Pleistoceno medio incluidas por muchos autores en *L. spelaeus*. Como ya apuntó Pons-Moyà (1985), seguramente estos restos de finales del Pleistoceno inferior representen los primeros estadios del linaje de *L. pardinus*. Aceptándose esta hipótesis, la presencia variable de ectostilo en el P4 sería esperable, de hecho uno de los autores (A.B) ha podido observar la presencia variable de ectoparastilo en bajos porcentages en todas las especies actuales del genero *Lynx*, siendo este carácter por tanto poco diagnóstico (*contra* Kurtén, 1978).

Mandíbula y dentición inferior: Los corpus mandibulares estudiados son más gráciles y bajos que los de *L. issiodorensis*, teniendo unas dimensiones y proporciones muy similares a los materiales de *L. spelaeus* del Pleistoceno medio y superior (Testu, 2006). Los dos p3 registrados presentan unas dimensiones relativamente pequeñas en relación a *L. issiodorensis*, en un caso se observa paraconido bien formado y en otro leve. En *Caracal* y *L. pardinus* esta cúspula normalmente está presente y acostumbra a ser reducida o estar ausente en *L. issiodorensis*. La morfología y proporciones son muy parecidas a *L. p. spelaeus* (Tabla 6). Los p4 presentan las dos cúspides accesorias bien desarrolladas y protocónido alto y cortante. Estas características son comunes en *L. issiodorensis* y *L. pardinus* pero el material estudiado muestra unas dimensiones más próximas a la segunda especie. *Caracal* acostumbra a presentar las mismas dimensiones, pero con protocónido más alto y esbelto. La ausencia total de metacónido y talónido en el m1 de dos de los ejemplares estudiados, así como la presencia de un leve repliegue de esmalte en el otro, asemeja el material de Cueva Victoria a *L. pardinus* y lo diferencia de *L. issiodorensis* y *L. spelaeus*, donde la presencia de talónido reducido y metacónido vestigial es habitual (Pons-Moyà, 1985; Morales et al., 2003; Testu, 2006). Una característica adicional que diferencia el material de Cueva Victoria de *L. spelaeus* es la reducción del cíngulo distal del p4 característico de la última especie (Testu, 2006). Igual que en el caso de la dentición anterior, la variabilidad observada en el desarrollo del parastilo del p2 y la reducción prácticamente total de metacónido y talónido en los m1 de la muestra hace pensar que nuestros especímenes corresponden a una forma arcaica de *L. pardinus*.

Esqueleto postcraneal: Las dos escápulas estudiadas presentan fosa glenoidea subcircular y apófisis coracoides ligeramente expandida medialmente. Esta condición es observada también en *L. pardinus,* siendo mucha más alargada en dirección medial en *Caracal depereti* y *C. caracal* (Morales et al., 2003). El húmero estudiado presenta reducción de los epicóndilos marcada y superficie articular dividida en dos por una depresión estrecha y profunda como en *L. pardinus* (Morales et al., 2003). Los dos fragmentos de radio estudiados presentan una morfología muy cercana a *L. pardinus* con una tuberosidad radial alargada, donde se puede observar la presencia de una pequeña tuberosidad palmar (Morales et al., 2003; Testu, 2006). El quinto metacarpiano es de morfología muy cercana a *L. pardinus* con faceta proximal no inclinada y semicircular, y diáfisis sin torsión lateral. Los fragmentos distales de tibia presentan una epífisis distal de contorno trapezoidal, los maléolos bien desarrollados y las facetas articulares del astrágalo poco marcadas. Estos caracteres son compartidos con *L. pardinus*. El tercer y quinto metatarsianos igualmente, muestran muchas similitudes en dimensiones y morfología con *L. pardinus*, con facetas de articulación ligeramente convexas para la articulación de los huesos del tarso y diáfisis muy rectilínias o con una muy ligera torsión dorso-palmar.

CONCLUSIONES

En el presente trabajo se hace una revisión del material de las familias Ursidae, Hyaenidae y Felidae, recuperado durante los últimos treinta años de excavaciones en el yacimiento del Pleistoceno inferior de Cueva Victoria en Cartagena (Murcia). El material estudiado ha permitido identificar las siguientes especies: *Ursus deningeri, Pachycrocuta brevirostris, Homotherium latidens, Megantereon* sp., *Panthera gombaszoegensis, Puma pardoides* y *Lynx pardinus*. La anterior asociación es característica de los yacimientos del Pleistoceno inferior final del área mediterránea y, en concreto, del biocron conocido como Epivillafranchiense con una cronología aproximada de 1.1-0.78 Ma. Esta misma asociación de especies ha sido descrita en otros yacimientos europeos como Untermassfeld (Alemania), Vallonnet (Francia) y en diferentes niveles de los yacimientos ibéricos de la Sección de Vallparadís.

La presencia de formas arcaicas de las especies *U. deningeri* y *L. pardinus*, no registradas hasta la fecha en yacimientos con cronologías anteriores al millón de años (OIS31) es muy significativa. De igual forma, la identificación del género *Megantereon* aporta una valiosa información. Los últimos registros conocidos de este género corresponden a las localidades de Untermassfeld y Vallparadís Estació EVT10, ambos con una cronología de ca. 1 Ma (OIS31).

En base a los datos anteriores se puede concluir que la acumulación de Cueva Victoria tiene una edad comprendida entre 1.1-0.78 Ma. Si se tienen en cuenta los últimos y primeros registros conocidos de las especies *U. deningeri, L. pardinus* y *Megantereon* esta cronología se podría precisar en torno a ca. 1 Ma.

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REFERENCIAS

AGUSTÍ, J., 1982: Los roedores (Mammalia) del Pleistoceno inferior de la Cueva Victoria (Murcia, España). *Endins*, 9, pp. 49-55.

ALCALDE, G.; AGUSTÍ, J.; VILLALTA, J. F., 1981: Un nuevo *Allophaiomys* (Arvicolidae, Rodentia, Mammalia) en el Pleistoceno Inferior del sur de España. *Acta Geológica Hispánica*, 16, pp. 203-205.

ARGANT, A., 1991: Carnivores Quaternaries de Bourgogne. *Documents des Laboratoires de Géologie du Lyon*, 115, pp. 1-301.

ARGANT, A., 2006: Ancient bears. *Proceedings of the 12th International Cave Bear Symposium*, Aridea, Macedonia, Greece, pp. 45-46.

ARGANT, A.; ARGANT, J.; JEANNET, M.; ERBAJEVA, K., 2007: The big cats of the fossil site Château Breccia Northern Section (Saône-et-Loire, Burgundy, France): stratigraphy, palaeoenvironment, ethology and bio-chronological dating. En: R. D. Kahlke; L. C. Maul; P. P. A. Mazza (eds.), *Late Neogene and Quaternary biodiversity and evolution: Regional developments and interregional correlations*. Proceedings of the 18th International Senckenberg Conference (VI International Palaeontological Colloquium in Weimar), Volume II. *Courier Forschungsinstitut Senckenberg*, 259, pp. 121-140.

ARRIBAS, A.; GARRIDO, G., 2008: Hiénidos [*Pachycrocuta brevirostris* (Aymard, 1846) y *Hyaena brunnea* Thunberg, 1820] del yacimiento de Fonelas P-1 (Cuenca de Guadix, Granada). En: A. Arribas (Ed.), *Vertebrados del Plioceno superior terminal en el suroeste de Europa. Fonelas P-1 y el Proyecto Fonelas*. *Cuadernos del Museo Geominero*, 10, pp. 201-230.

BALLESIO, R., 1963: Monographie d'un *Machairodus* du gisement villafranchien de Senêze: *Homotherium cre-*

natidens Fabrini. *Travaux Laboratoire Géologie Lyon*, 9, pp. 1-129.

BALLESIO, R., 1986: Les Carnivores du gisement Pléistocène d'Oubéidiyeh. En: E. Tchernov, (Ed.) *Les Mammifères du Pléistocène Inférieur de la Vallée du Jourdain a Oubéidiyeh*, Assoc. Paléorient, París, pp. 63-92

BLAIN, H. A.; BAILÓN, S.; AGUSTÍ, J., 2008: Amphibians and squamate reptiles from the latest Early Pleistocene of Cueva Victoria (Murcia, Southeastern Spain, SW Mediterranean): Paleobiogeographic and paleoclimatic implications. *Geologica Acta*, 6, pp. 345-361.

BONIFAY, M. F., 1971: Carnivores quaternaries du Sud-Est de la France. *Mémoires du Muséum National d'Historie Naturelle Nouvelle Série C,* 21, pp. 1-377.

CARBONELL, E.; ESTÉVEZ, J.; MOYÀ-SOLÀ, S.; PONS-MOYÀ, J.; AGUSTÍ, J.; VILLALTA, J. F., 1981: «Cueva Victoria» (Murcia, España): Lugar de ocupación humana más antiguo de la Península Ibérica. *Endins*, 8, pp. 47-57.

CIPULLO, A., 2010: *L'evoluzione del genere Lynx dal Pliocene al Pleistocene Medio nell'area mediterranea*. PhD Thesis. Modena-Bologna-Roma Universities.

CHERIN, M.; IURINO, D. A.; SARDELLA, R., 2013: Earliest occurrence of *Puma pardoides* (Owen, 1846) (Carnivora, Felidae) at the Plio/Pleistocene transition in western Europe: New evidence from the Middle Villafranchian assemblage of Montopoli, Italy. *Comptes Rendus Palevol*, 12, pp. 165-171.

CHRISTIANSEN, P.; ADOLFSSEN, J. S., 2007: Osteology and ecology of *Megantereon cultridens* SE311 (Mammalia; Felidae; Machairodontidae), a sabrecat from the Late Pliocene-Early Pleistocene of Senèze, France. *Zoological Journal Linnean Society*, 151, pp. 833-884.

FERRÁNDEZ, C.; PÉREZ-CUADRADO, J. L.; GIBERT, J.; MARTÍNEZ, B., 1989: Estudio preliminar de los sedimentos de relleno de Cueva Victoria (Cartagena, Murcia), en: J. Gibert; D. Campillo; E. García Olivares (eds.) *Los restos humanos de Orce y Cueva Victoria* (eds.), Publicacions de l'Institut de Paleontologia Dr. M. Crusafont, Barcelona, pp. 379-393.

FICARRELLI, G., 1979: The Villafranchian machairodonts of Tuscany. *Palaeontographia Italica,* 71, pp. 17-26.

FICCARELLI, G.; TORRE, D., 1968: Upper Villafranchian panthers of Tuscany. *Palaeontographia Italica*, 64, pp. 173-184.

FICCARELLI, G.; TORRE, D., 1977: Phyletic relationship between *Lynx* Group *issiodorensis* and *Lynx pardina. Bollettino della Società Paleontologica Italiana,* 16, pp. 197-202.

GALOBART, À.; ANTÓN, M.; MAROTO. J., 2003a: Hiénidos y cánidos de los yacimientos de Incarcal (Girona, NE de la Península Ibérica). Una aproximación a la paleobiología del hiénido del Pleistoceno inferior. *Paleontologia i Evolució*, 34, pp. 79-98.

GALOBART, À.; PONS-MOYÀ, J.; ANTÓN, M.; MAROTO, J., 2003b: Descripción del material de *Homotherium latidens* (Owen) de los yacimentos del Pleistoceno inferior de Incarcal (Girona, NE de la Penísula Ibérica). *Paleontologia i Evolució*, 34, pp. 99-141

GARCÍA, N., 2003: *Osos y otros carnívoros de la sierra de Atapuerca*. Fundación Oso de Asturias, Oviedo, 576 pp.

GARCÍA, N.; ARSUAGA, J. L., 2001: *Ursus dolinensis*: a new species of Early Pleistocene ursid from Trinchera Dolina, Atapuerca (Spain). *Comptes Rendus de l'Academie des Sciencies de Paris*, 332, pp. 717-725.

GIBERT, J. (ed.), 1992: *Presencia humana en el Pleistoceno inferior de Granada y Murcia*. Museo de Prehistoria y Paleontología J. Gibert, Orce.

GIBERT, J., 1999: Significado de la fauna de Cueva Victoria. *Memorias de Arqueología Región de Murcia*, 8, pp. 26-32.

GIBERT, J., 2004: Cueva Victoria: Puerta de Europa. *Memorias de Arqueología, Región de Murcia*, 12, pp. 29-36.

GIBERT, J.; CAMPILLO, D.; GARCÍA OLIVARES, E. (eds.), 1989: *Los restos humanos de Orce y Cueva Victoria*. Instituto de Paleontología Dr. M. Crusafont, Diputació de Barcelona, Barcelona.

GIBERT, J.; MARTÍNEZ, B.; CAPORICCI, R.; JIMÉNEZ, C.; FERRÁNDEZ, C.; RIBOT, F.; SORIA., F.; PÉREZ-CUADRADO, J. L.; ARRIBAS, A.; CANALS, J.; GARCÍA-TARGA, J. M.; IGLESIAS, A.; ROMERO, R., 1988: Resumen de las investigaciones paleoantropológicas y arqueológicas de Orce (Granada) y Cueva Victoria (Cartagena). *COL-PA, Publicaciones del departamento de Paleontología*, 42, pp. 11-61.

GIBERT, J.; FERRÁNDEZ, C.; PÉREZ-CUADRADO, J. L.; MARTÍNEZ, B., 1992: Cueva Victoria: Cubil de carroñeros, en: J. Gibert (coord.), *Proyecto Orce-Cueva Victoria 1988-1992, Presencia humana en el Pleistoceno inferior de Granada y Murcia*. Museo de Prehistoria de Orce, Orce (Granada), pp. 133-142.

GIBERT, J.; GIBERT, L.; FERRÁNDEZ, C.; RIBOT, F.; IGLESIAS, A.; GIBERT, P., 2006: Cueva Victoria: Geología, Paleontología, restos humanos y edades. *Memorias de Arqueología Región de Murcia*, 14 (1999), pp. 37-62.

GILES-PACHECO, F.; SANTIAGO, A.; GUTIÉRREZ, J. L.; LÓPEZ-GARCÍA, J. M.; BLAIN, H. A.; CUENCA-BESCÓS, G., VAN DER MADE, J.; CÁCERES, I.; GARCÍA, N., 2011: The Early Pleistocene paleontological site in the Sierra del Chaparral (Villaluenga de Rosario, Cádiz, Southwestern Spain). *Quaternary International*, 243, pp. 92-104.

GLIOZZI, E.; ABBAZI, L.; AMBROSETTI, P.; ARGENTI, P.; AZZAROLI, A.; CALOI, L.; CAPASSO BARBATO, L.; DI STEFANO, G.; ESU, D.; FICCARELLI, G.; GIROTTI, O.; KOTSAKIS, T.; MASINI, F.; MAZZA, P.; MEZZABOTTA, C.; PALOMBO, M. R.; PETRONIO, C.; ROOK, L.; SALA, B.; SARDELLA, R.; ZANALDA, E.; TORRE, D., 1997: Biochronology of selected mammals, molluscs, ostracods from the Middle Pliocene to the Late Pleistocene in Italy. The state of the art. *Rivista Italiana di Paleontologia e Stratigrafia*, 103, pp. 369-388.

HEMMER, H. (2001). Die Feliden aus dem Epivillafranchium von Untermassfeld. En: R. D. Kahlke (ed.), *Das Pleistozän von Untermassfeld bei Meiningen (Thüringen),* Römisch-Germaisches Zentralmuseum, Bonn, pp. 699-782.

HEMMER, H.; KAHLKE, R. D.; VEKUA, A, K., 2001: The jaguar *Panthera onca gombaszoegensis* (Kretzoi, 1938) (Carnivora: Felidae) in the late Lower Pleistocene of Akhalkalaki (South Georgia; Transcaucasia) and its evolutionary and ecological significance. *Geobios*, 34, pp. 475-486.

HEMMER, H.; KAHLKE, R. D.; VEKUA, A. K., 2010: *Panthera onca georgica* ssp. nov. from the Early Pleistocene of Dmanisi (Republic of Georgia) and the phylogeography of jaguars (Mammalia, Carnivora, Felidae). Neues Jahrbuch für Geologie und Paläontologie- Abhandlungen, 257, pp. 115-127.

HUGUENEY, M.; GUÉRIN, C.; POIDEVIN, J. L., 1989: Découverte de *Trogontherium minus* Newton 1890 (Rodentia: Castoridae) dans le Villafranchien inférieur de Perrier- Étouaires (Puy-de-Dôme, France): implications phylogénétiques. *Comptes Rendus Academie des Sciencies Paris*, 309, pp. 763-768.

KAHLKE, R. D., 2006: *Untermassfeld - A late Early Pleistocene (Epivillafranchian) fossil site near Meiningen (Thuringia, Germany) and its position in the development of the European mammal fauna*. BAR International Series 1578, Archaeopress, Oxford, 141 pp.

KOENIGSWALD, W. VON; NAGEL, D.; MENGER, F., 2006: Ein jungpleistozäner Leopardenkiefer von Geinsheim (nördliche Oberrheinebene) und die stratigraphische und ökologische Verbreitung von *Panthera pardus*. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 5, pp. 277-297.

KOUFOS, G. D., 1992: The Pleistocene carnivores of the Mygdonia basin (Macedonia, Greece), *Annales de Paléontologie*, 78, pp. 205-257.

KURTÉN, B., 1968: *Pleistocene Mammals of Europe*. Weidenfeld and Nicholson, London, 317 pp.

KURTÉN, B., 1978: The Lynx from Etouaires, *Lynx issiodorensis* (Croizet y Jobert), late Pliocene. *Annales Zoologici Fennici*, 15, pp. 314-322.

MADURELL-MALAPEIRA, J., 2010: *The Villafranchian Carnivores from the North-eastern Iberian Península and the Early-Middle Pleistocene Transition*. Ph. D. Thesis. Universitat Autònoma de Barcelona, Cerdanyola del Vallès, 224 pp.

MADURELL-MALAPEIRA J.; ALBA, D. M.; MOYÀ-SOLÀ, S., 2009: Carnivora from the late Early Pleistocene of

Cal Guardiola (Terrassa, Vallès-Pendès Basin, Catalonia, Spain). *Journal of Paleontology*, 83, pp. 969-974.

MADURELL-MALAPEIRA, J.; MINWER-BARAKAT, R.; MARTÍNEZ ALBA, D.; GARCÉS, M.; GÓMEZ, M.; AURELL-GARRIDO, J.; MOYÀ-SOLÀ, S.; BERÁSTEGUI, X., 2010a: The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe. *Quaternary Science Reviews,* 29, pp. 3972-3982.

MADURELL-MALAPEIRA, J.; ALBA, D. M.; MOYÀ-SOLÀ, S.; AURELL-GARRIDO, J., 2010b: The Iberian record of the puma-like cat *Puma pardoides* (Owen, 1846). *Comptes Rendus Palevol*, 9, pp. 55-62.

MADURELL-MALAPEIRA, J.; ROS MONTOYA, S.; ESPIGARES, M. P.; ALBA, D. M.; AURELL-GARRIDO, J., 2014: Villafranchian large mammals from the Iberian Peninsula: Paleogeography, paleoecology and dispersal events. *Journal of Iberian Geology,* 40 (1)*,* pp. 141-155*.*

MARTIN, R. A., 2012: *Victoriamys*, a new generic name for Chaline's vole from the Pleistocene of Western Europe. *Geobios*, 45, pp. 445-450.

MARTÍNEZ NAVARRO, B.; PALMQVIST, P., 1995: Presence of the African machairodont *Megantereon whitei* (Broom 1937) (Felidae, Carnivora, Mammalia) in the Lower Pleistocene site of Venta Micena (Orce, Granada, Spain), with some considerations on the origin, evolution and dispersal of the genus. *Journal of Archaeological Science*, 22, pp. 569-582.

MARTÍNEZ-NAVARRO, B.; PALMQVIST, P., 1996: Presence of the African saber-toothed felid *Megantereon whitei* (Broom, 1937) (Mammalia, Carnivora, Machairodontinae) in Apollonia-1 (Mygdonia Basin, Macedonia, Greece). *Journal of Archaeological Science,* 23, pp. 869-872.

MARTÍNEZ-NAVARRO, B.; BELMAKER, M.; BAR-YOSEF, O., 2009: The large carnivores from 'Uberidiya (early Pleistocene, Israel): biochronological and biogeographical implications. *Journal of Human Evolution*, 56, pp. 514-524.

MORALES, J.; SORIA, D.; SOTO, E., 1987: Los carnivoros del Pleistoceno medio de Atapuerca. En: E. Aguirre; E. Carbonell; J. M. Bermúdez de Castro (eds.), *El hombre fósil de Ibeas y el Pleistoceno de la Sierra de Atapuerca,* Junta de Castilla y León, Valladolid, pp. 135-151.

MORALES, J.; SORIA, D.; MONTOYA, P.; PÉREZ, B.; SALESA, M. J., 2003: *Caracal depereti* nov. sp. y *Felis* aff. *silvestris* (Felidae, Mammalia) del Plioceno inferior de Layna (Soria, España). *Estudios Geológicos,* 59, pp. 229-247.

MOIGNE, A.M., PALOMBO, M.R., BELDA, V., HERIECH-BRIKI, D., KACIMI, S., LACOMBAT, F., DE LUMLEY, M.A., MOUTOUSSAMY, J., RIVALS, F., QUILÈS, J., TESTU, A., 2006: Les faunes de grands mammifères de la Caune de l'Arago (Tautavel) dans le cadre biochronologique des faunes du Pléistocène moyen italien. *L'Anthropologie,* 110, pp. 788-831.

MOULLÉ, P.E. , 1992: *Les grands mammifères du Pléistocene inférieur de la grotte du Vallonnet (Roquebrunne, Cap Martín, Alpes Maritimes).* Étude paléontologique des Carnivores, Equidae, Suidae et Bovidae. Ph.D. thesis. Muséum National d'Historie Naturelle, Paris.

MOULLÉ, P.E., LACOMBAT, F., ECHASSOUX, A., 2006: Apport des grands mammifères de la grotte du Vallonnet (Roquebrune-Cap-Martin, Alpes-Maritimes, France) à la connaissance du biochronologique de la seconde moité du Pléistocene inférieur d'Europe. *L'Anthropologie*, 110, pp. 837-849.

MUSIL, R., 2001: Die Ursiden-Resten aus dem Unterplesitozän von Untermassfeld. *Das Pleistozän von Untermassfeld bei Meiningen (Thüringen),* pp. 557-587. Römisch-Germaisches Zentralmuseum, Bonn. R.D. Kahlke, Ed.

OLIVE, F., 2006: Évolution des grands Carnivores au Plio Pléistocene en Afrique et en Europe occidentale. *L'Anthropologie*, 110, pp. 850-869.

O'REGAN, H.; TURNER, A., 2004: Biostratigraphic and palaeoecological implications of new fossil felid material from the Plio-Pleistocene site of Tegelen, The Netherlands. *Palaeontology*, 47, pp. 1181-1193.

PALMQVIST, P., MARTÍNEZ-NAVARRO, B., TORO, I., ESPIGARES, M.P., ROS-MONTOYA, S., TORREGROSA, V., PÉREZ-CLAROS, J. (2005). A re-evaluation of the evidence of human presence during Early Pleistocene times in southeastern Spain. *L'Anthropologie*, 109, pp. 411-450.

PALMQVIST, P., TORREGROSA, V., PÉREZ-CLAROS, J.A., MARTÍNEZ-NAVARRO, B., TURNER, A., 2007: A re-evaluation of the diversity of *Megantereon* (Mammalia, Carnivora, Machairodontinae) and the problem of species identification in extinct carnivores. *Journal of Vertebrate Paleontology*, 27, pp. 160-175.

PALMQVIST, P., MARTÍNEZ-NAVARRO, B., PÉREZ-CLAROS, J.A., TORREGROSA, V., FIGUEIRIDO, B., JIMÉNEZ-ARENAS, J.M., ESPIGARES, M.P., ROS-MONTOYA, S., DE RENZI, M., 2011: The giant hyena *Pachycrocuta brevirostris*: modelling the bone-cracking behavior of an extinct carnivore. *Quaternary International*, 243, pp. 61-79.

PALOMBO, M.R., SARDELLA, R., NOVELLI, M., 2008: Carnivora dispersal in Western Mediterraenan during the last 2.6 Ma. *Quaternary International*, 179, pp. 72-78.

PEI, W.C. (1934). On the Carnivora from Locality 1 of Choukoutien. *Palaeontologia Sinica*, 8, pp. 1-166.

PETRONIO, C., DI CANZIO, E., DI STEFANO, G., 2003: Morphometrical and biometrical diferencies in the limb bones of *Ursus arctos* and *Ursus spelaeus* and phylogenetical considerations on the two species. *Palaeontographica A*, 269, pp. 137-152.

PETRUCCI, M., SARDELLA, R., 2009: *Ursus etruscus* Cuvier, 1823 from the Early Pleistocene of Monte Argentario (Southern Tuscany, Central Italy). *Bollettino della Società Paleontologica Italiana*, 48, pp. 89-94.

PETRUCCI, M., CIPULLO, A., MARTÍNEZ-NAVARRO, B., ROOK, L., SARDELLA, R., 2013: The Late Villafranchian (Early Pleistocene) carnivores (Carnivora, Mammalia) from Pirro Nord (Italy). *Palaeontographica A*, 298, pp. 113-145.

PONS-MOYÀ, J., 1981: El *Canis etruscus* Major (*Carnivora, Mammalia*) del Villafranquiense terminal de la Cueva Victoria (Murcia, España). *Endins*, 8, pp. 43-46.

PONS-MOYÀ, J., 1982: Hyaenidae (Carnivora, Mammalia) del Pleistoceno inferior de la Cueva Victoria (Murcia, España). *Endins*, 9, pp. 45-48.

PONS-MOYÀ, J., 1983: Presencia de *Lynx spelaea* (Fissipeda, Mammalia) en el Pleistoceno inferior de la Península Ibérica. *Paleontologia i Evolució*, 18, pp. 39-42.

PONS-MOYÀ, J., MOYÀ-SOLÀ, S. (1978). La fauna de carnívoros del Pleistoceno medio (Mindel) de la Cueva Victoria (Cartagena, España). *Acta Geologica Hispanica*, 13, pp. 54-58.

QIU, Z., DENG, T., WANG, B., 2004: Early Pleistocene mammalian fauna from Longdan, Dongxiang, Gansu, *China. Palaeontologia Sinica*, 191, pp. 1-198.

RABEDER, G., PACHER, M., WITHALM, G., 2010: *Early Pleistocene Bear remains from Deutch-Altenburg (Lower Austria)*. Mitteilungen der Kommission für Quartärforschung der Österreichischen Akademie der Wissenschaften, Band 17, Verlag der Österreichischen Akademie der Wissenschaften, Vienna.

REUMER, J.W.F., ROOK, L., VAN DER BORG, K., POST, K., MOL, D., DE VOS, J., 2003: Late Pleistocene survival of the sabertoothed cat *Homotherium* in Northwestern Europe. *Journal of Vertebrate Paleontology,* 23, pp. 260-262.

SARDELLA, R., 1998: The Plio-Pleistocene Old World dirk-toothed cat *Megantereon* ex gr. *cultridens* (Mammalia, Felidae, Machairodontinae), with comments on taxonomy, origin and evolution. *Neues Jahrbuch für Geologie und Paläontologie—Monatshefte*, 207, pp. 1-36.

TESTU, A., 2006: *Etude Paleontologique et bioestratigraphique des Felidae et Hyaenidae pléistocenes de l'Europe méditerranéenne*. PhD thesis. Université de Perpignan, Perpignan.

TORRES, T., 1984: Úrsidos del Pleistoceno-Holoceno de la Península Ibérica. PhD. Universidad Politécnica de Madrid, Madrid.

TORRES, T., 1992: Los restos de oso del yacimiento de Venta Micena (Orce, Granada) y el material de *Ursus etruscus* G. Cuvier del Villafranquiense europeo. *Presencia humana en el Pleistoceno Inferior de Granada y Murcia - Proyecto Orce- Cueva Victoria (1988-1992)*, pp. 87-96. Ayuntamento de Orce (Granada). J. Gibert, Ed.

TSOUKALA, E., 2004: The Early Pleistocene carnivores (Mammalia) from Ceyssaguet (Haute-Loire). *Paleo*, 16, pp. 193-242.

TURNER, A., 1987: *Megantereon cultridens* (Cuvier) (Mammalia, Felidae, Machairodontinae) from Plio-Pleistocene deposits in Africa and Eurasia, with comments on dispersal and the possibility of a new world origin. *Journal of Paleontology,* 61, pp. 1256-1268.

TURNER, A., 1999: Larger carnivores (Mammalia, Carnivora) from Westbury Cave, En: P. Andrews, Cook, J., Stringer, C., Currant, A., (eds.), *Westbury Cave: The Natural History Museum Excavations 1976-1984*, Bristol: Western Academic and Specialist Press, pp. 175-193.

TURNER, A., 2001: Remains of *Pachycrocuta brevirostris* (Carnivora, Hyaenidae) from the Lower Pleistocene site of Untermassfeld. *Das Pleistozän von Untermassfeld bei Meiningen (Thüringen)*, pp. 673-690. Römisch-Germaisches Zentralmuseum, Bonn. R. D. Kahlke, Ed.

TURNER, A., ANTÓN, M., 1996: The giant hyaena *Pachycrocuta brevirostris* (Mammalia, Carnivora, Hyaenidae). *Geobios*, 29, pp. 455-468.

TURNER, A., ANTÓN, M., 1997: *The big cats and their fossil relatives*. Columbia University Press, New York.

VALENZUELA, A., 1970: Un karst fósil y depósitos minerales de origen cárstico. al sureste de la zona Bética. *Comunicaciones del primer Congreso Nacional de Espeleologia*, pp. 61-77.

VIRET, J. (1954). Le loess à bancs durcis de Saint-Vallier (Drôme) et sa faune de mammifères villafranchiens. *Nouvelles Archives du Museum d'Histoire naturelle de Lyon*, 4, pp. 1-200.

WERDELIN, L., 1981: The evolution of lynxes. *Annales Zoologici Fennici*, 18, pp. 37-71.

Chapter 7. Were large carnivorans and great climatic shifts limiting factors for hominin dispersals? Evidence of the activity of *Pachycrocuta brevirostris* during the Mid-Pleistocene Revolution in the Vallparadís Section (Vallès-Penedès Basin, Iberian Peninsula).

Reference: Madurell-Malapeira, J., Alba, D.M., Espigares, M.P., Vinuesa, V., Palmqvist, P., Martínez-Navarro, B., & Moyà-Solà, S. (2017). Were large carnivorans and great climatic shifts limiting factors for hominin dispersals? Evidence of the activity of *Pachycrocuta brevirostris* during the Mid-Pleistocene Revolution in the Vallparadís Section (Vallès-Penedès Basin, Iberian Peninsula). *Quaternary International 431*, 42–52.

Summary: This work analyzes how carnivores would have limited food availability to early European human populations, by focusing on the Vallparadís section. In particular, the scavenging habits of the Villafranchian hyena, *Pachycrocuta brevirostris*, are studied based on the taphonomic analysis of herbivore remains.

Author's contribution: The doctoral candidate participates in this work as coauthor (4th position). He was involved in fossil data collection and analysis (including graphics and figures), and revised the whole manuscript.

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Were large carnivorans and great climatic shifts limiting factors for hominin dispersals? Evidence of the activity of *Pachycrocuta brevirostris* during the Mid-Pleistocene Revolution in the Vallparadís Section (Vallès-Penedès Basin, Iberian Peninsula)

Joan Madurell-Malapeira [a, *], David M. Alba [a], María-Patrocinio Espigares [b, c], Víctor Vinuesa [a], Paul Palmqvist [b], Bienvenido Martínez-Navarro [d, e], Salvador Moyà-Solà [f]

[a] *Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, Carrer de les Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain*
[b] *Departamento de Geología y Ecología, Universidad de Málaga, Campus de Teatinos, 29071 Málaga, Spain*
[c] *Museo de Prehistoria y Paleontología, 18858 Orce, Granada, Spain*
[d] *ICREA at Institut Català de Paleoecologia Humana i Evolució Social, c/Marcel·lí Domingo s/n, Edifici W3, Campus Sescelades URV, 43007 Tarragona, Spain*
[e] *Àrea de Prehistoria, Universitat Rovira i Virgili, Avda. Catalunya 35, 43002 Tarragona, Spain*
[f] *ICREA at Institut Català de Paleontologia Miquel Crusafont and Unitat d'Antropologia (Dept. BABVE), Universitat Autònoma de Barcelona, Edifici ICTA-ICP, Carrer de les Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain*

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ABSTRACT

The chronology of the first human dispersal out of Africa and the ecological role of the genus *Homo* in Europe as a scavenger or an active hunter during the late Early Pleistocene are two of the paleoanthropological topics most hotly debated during the last decades. The earliest human occurrences in Western Europe are recorded in the Iberian Peninsula by the late Villafranchian (1.4–1.2 Ma), during a period of climatic stability. However, currently available taphonomic and paleoecological data suggest a direct and intense competition for food resources between these human populations and the large scavenging hyaenid *Pachycrocuta brevirostris*. The Villafranchian was followed by the Epivillafranchian (ca. 1.2–0.8 Ma), a period of climatic instability dominated by several strong glacial periods. The evidence from the Vallparadís Section reported here suggests that such unstable climatic conditions did not affect to a great extent the composition of the large mammal assemblages and, particularly, that of the carnivore guild. Based on the impressive record of carnivoran remains recovered from the Vallparadís Section and the taphonomic interpretation of this assemblage, we suggest that the putative direct competition between early *Homo* and large carnivores, especially *P. brevirostris*, persisted throughout the late Villafranchian and the Epivillafranchian.

1. Introduction

The oldest evidence of hominin presence in the Iberian Peninsula comes from three localities, Barranco León and Fuente Nueva-3 in the Guadix-Baza Basin and Sima del Elefante in the Atapuerca karst complex, which are dated to the latest Early Pleistocene (ca. 1.4–1.2 Ma; Martínez-Navarro et al., 1997; Carbonell et al., 2008; Palmqvist et al., 2005; Espigares et al., 2013; Toro-Moyano et al., 2013). In Iberia, this time interval was characterized by warm temperatures and landscapes dominated by open dry grasslands with tree patches (Mendoza et al., 2005; Leroy et al., 2011). Of these landscapes, the Guadix-Baza Basin represented a hot spot or ecological island for vertebrate diversity developed in the surroundings of a lake subject to hydrothermal feeding (García-Aguilar et al., 2014, 2015).

Several authors have suggested that the paleoenvironmental conditions most favorable for the dispersal of hominins across Europe would correspond to open landscapes, similar to the African environments in which the early members of *Homo* evolved. The Iberian Peninsula apparently displayed such environments,

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* Corresponding author.
E-mail address: joan.madurell@icp.cat (J. Madurell-Malapeira).

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although other factors might have conditioned the survival of these human populations. In particular, taphonomic studies carried out in the Orce localities suggest that large scavenging carnivorans, such as the giant, short-faced hyena *Pachycrocuta brevirostris*, were responsible of an intense bone modification activity during the late Early Pleistocene (Arribas and Palmqvist, 1998; Espigares, 2010; Palmqvist et al., 2011; Espigares et al., 2013). Evidence of anthropic action on bones is also recorded at these sites (Espigares et al., 2013; Toro-Moyano et al., 2013), although the analysis of data at hand suggests that primary access to ungulate carcasses by humans took only place under occasional circumstances, for example those recorded at Fuente Nueva-3, where intense competition between humans and hyenas around an elephant carcass has been documented (Espigares et al., 2013). Several scholars have established a parallelism between the composition of the large carnivore guild and the impact of hominin activities in the fossil record (e.g., Turner, 1992; Turner and Antón, 1998; Rodríguez et al., 2012; Rodríguez-Gómez et al., 2013). As a result, hominin activities seem to have had a much scarcer impact in the localities with Villafranchian carnivorans than in those with Galerian carnivorans (Madurell-Malapeira et al., 2010, 2014).

Shortly after the record of the Guadix-Baza Basin, a global climatic event, known as the Mid-Pleistocene Revolution (MPR) and elapsing from 1.25 Ma to 0.7 Ma, started in the Northern Hemisphere (Clark et al., 2006). During this time interval, the previous low-amplitude, 41 ky obliquity-forced climate cycles were progressively replaced by high-amplitude, 100 ky cycles related to changes in the eccentricity of the Earth's orbit. This implied a transition towards a strongly non-linear forced climate system, and was accompanied by a substantial increase in global ice volume at 0.94 Ma (Clark et al., 2006). Such climatic changes had a profound effect on the biota and the physical landscape, and, as a consequence, probably also in the interaction of European early *Homo* with the environment and the carnivore guild (Palombo, 2014).

There are only a few European localities that record this time interval of marked climatic shifts, thereby enabling the study their impact on the composition of vertebrate taphocenoses. The Vallparadís Section (Vallès-Penedès Basin) is chronologically well constrained (ranging from 1.2 to 0.6 Ma) and records the same carnivore guild as the Orce localities during the MPR, at last until 0.86 Ma (Madurell-Malapeira et al., 2010, 2014). This evidence suggests that, in the Iberian Peninsula, the carnivore guild remained stable during the late Villafranchian and Epivillafranchian. In this paper, we review the evidence of activity of *P. brevirostris* in the different layers of the Vallparadís Section and compare it with the activity of this carnivoran documented at the Orce sites.

2. Vallparadís Section

2.1. Geological background

The Vallparadís composite section includes the paleontological sites of Cal Guardiola and Vallparadís Estació, which are situated in the western and eastern bank, respectively, of the Torrent de Vallparadís, within the town of Terrassa (el Vallès Occidental, Catalonia, Spain; Fig. 1). The Quaternary deposits of Cal Guardiola and Vallparadís Estació correspond to the Pleistocene alluvial fan system of Terrassa (Berástegui and Losantos, 2001), which overlies a marked Miocene paleorelief. The sediments of the Cal Guardiola site consist of a 7 m-thick unit of massive conglomerates and gravels in a matrix-supported fabric (Fig. 2). The beds are about 1 m-thick and rich in fossils of animals and plants. The fossils are mainly concentrated in two units: a green unit (CGRD7) and a black unit (CGRD2) interbedded within the above-mentioned conglomerates and gravels (Berástegui et al., 2000). In the Vallparadís Estació site, there is a 14 m-thick sedimentary sequence, which is mainly composed of conglomerates and mudstones arranged in two units that are separated by an erosive angular unconformity (Fig. 2). The lower unit (layers EVT6 to EVT12) is made up of clast-supported, rounded, polymictic and poorly-sorted conglomerate beds that hardly attain 1 m of thickness. The conglomerates are intercalated with massive red mudstones that show root marks. The upper Unit (layers EVT1 to EVT5) begins with poorly sorted conglomerates and breccias that show an erosive lower contact. This bed is 1 m-thick, its fabric is clast-supported, and laterally passes into mudstones. Massive brownish mudstones with paleosols, root-marks and freshwater gastropods outcrop at the top of this unit. In this upper unit, there are also well-sorted conglomerates and sandstones with cross-lamination.

2.2. Chronology

On the basis of magnetostratigraphic and biostratigraphic data, the composite section of Vallparadís, formed by the local Cal Guardiola and Vallparadís Estació stratigraphic sequences, spans from before the Jaramillo paleomagnetic subchron to the early Middle Pleistocene (ca. 1.2–0.6 Ma; Fig. 2; Madurell-Malapeira et al., 2010; Minwer-Barakat et al., 2011). This time span can be divided into four intervals (Fig. 2): (R1) pre-Jaramillo times, only recorded in the Cal Guardiola sequence (layers CGRD1 to CGRD3), with a reversed paleomagnetic polarity; (N1) the Jaramillo subchron, only recorded in the Vallparadís Estació sequence (bottom of layer EVT8, and layers EVT9 to EVT12), with a normal polarity; (R2) post-Jaramillo, Matuyama times, with a reversed polarity, recorded both at Vallparadís Estació (bottom of layer EVT3, layers EVT4 to EVT7 and the top of layer EVT8) and Cal Guardiola (layers CGRD4 to CGRD8); and (N2) early Middle Pleistocene times, only recorded in the uppermost layers of the Vallparadís Estació sequence (EVT2 and EVT3), with a normal polarity that corresponds to the beginning of the Brunhes chron (Madurell-Malapeira et al., 2010, 2014; Minwer-Barakat et al., 2011).

2.3. Studied layers

The Vallparadís sequence includes more than ten layers from which large mammal remains have been recovered in an excellent state of preservation. Within these horizons, layers CGRD2 and CGRD7 of Cal Guardiola, and layers EVT3, EVT7 and EVT12 of Vallparadís Estació are the richest. More than 30,000 large mammal remains were unearthed from these layers, although only 8000 have been prepared and studied for the moment. For this reason, we only include in the present study those layers from which a significant number of specimens have been studied, namely CGRD2, CGRD7 and EVT7.

2.3.1. Layer CGRD2

This layer is included in the pre-Jaramillo lower unit of the Cal Guardiola local section, with an estimated age of ca. 1.2–1.1 Ma (Madurell-Malapeira et al., 2010, 2014). It yielded 937 large mammal remains, of which 431 (46.0%) are currently prepared for study. Of these, the number of identifiable specimens (NISP) is 325, which represents 34.7% of all recovered fossils. The following mammals have been identified from this layer (Madurell-Malapeira et al., 2010, 2014; J. M.-M., unpublished data): *Ursus deningeri*, *P. brevirostris*, *Homotherium latidens*, *Canis mosbachensis*, *Vulpes praeglacialis*, *Mammuthus* sp., *Hippopotamus antiquus*, *Bison* sp., *Megaloceros savini*, *Dama vallonnetensis*, *Stephanorhinus hundsheimensis*, *Equus altidens*, and *Mimomys savini*.

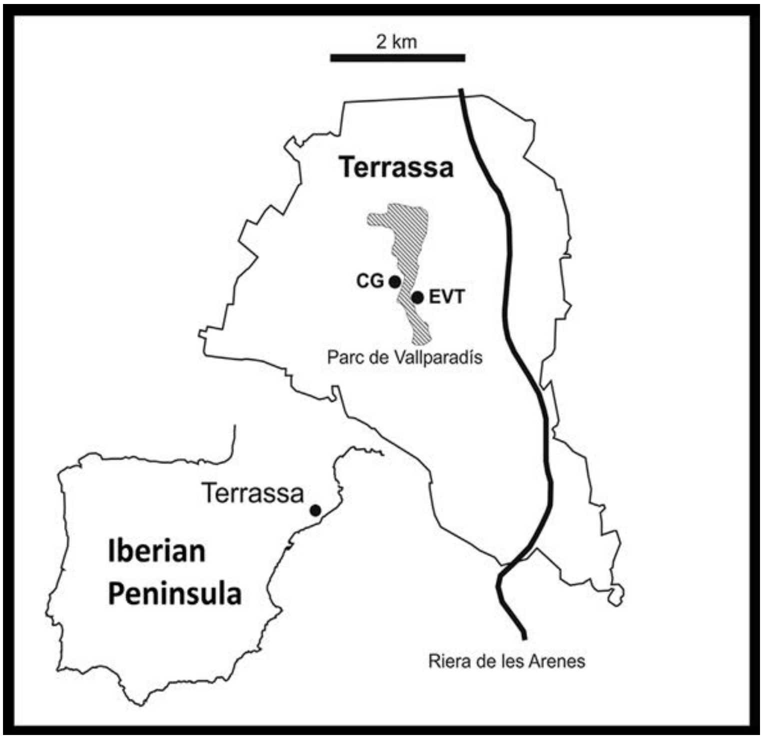

Fig. 1. Location map of the two localities of the Vallparadís Section within the Iberian Peninsula and the city of Terrassa.

2.3.2. Layer CGDD7

This layer of the Cal Guardiola local sequence is included in the post-Jaramillo interval of the Matuyama chron (ca. 0.99–0.78 Ma; Madurell-Malapeira et al., 2010, 2014). It yielded 748 large mammal remains, of which 639 are currently prepared for study (NISP = 588, 74.6% of all recovered fossils). The following mammals have been identified from this layer (Madurell-Malapeira et al., 2010, 2014; J. M.-M., unpublished data): *Macaca sylvanus* cf. *florentina*, *U. deningeri*, *P. brevirostris*, *Panthera gombaszoegensis*, *C. mosbachensis*, *Mammuthus* sp., *H. antiquus*, *Bison* sp., *D. vallonnetensis*, *S. hundsheimensis*, *E. altidens*, and *Me. savini*.

2.3.3. Layer EVT7

This layer of the Vallparadís local sequence is included in the post-Jaramillo interval of the Matuyama chron (ca. 0.99–0.78 Ma). An absolute date of 0.858 ± 0.087 Ma was obtained for this layer based on the ESR method (Duval et al., 2015), which probably corresponds to the interglacial stage MIS21 (Madurell-Malapeira

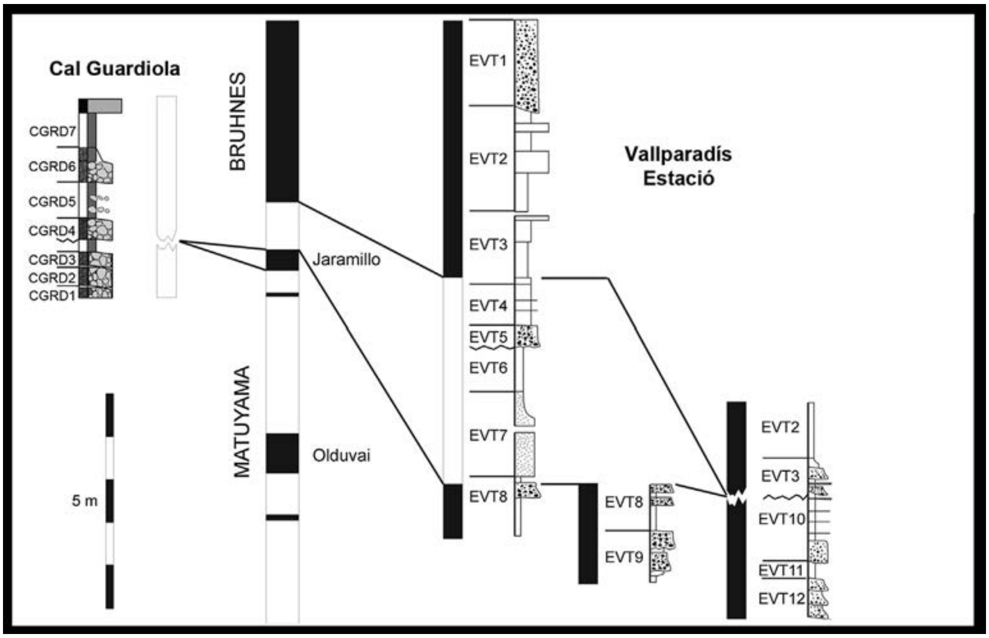

Fig. 2. Correlation of the magnestostratigraphy of the Vallparadís Section with the geomagnetic polarity time scale.

et al., 2010). This layer yielded 20,286 vertebrate remains, of which 3234 (16.0%) are currently prepared for study (NISP = 2,508, 12.4% of all recovered fossils). The following mammals have been identified from this layer (Madurell-Malapeira et al., 2010, 2014; Boscaini, 2014): *M. sylvanus* cf. florentina, *P. brevirostris*, *Meles meles atavus*, *U. deningeri*, *Lycaon lycaonoides*, *C. mosbachensis*, *V. praeglacialis*, *P. gombaszoegensis*, *Puma pardoides*, Felidae indet. (large form), *Lynx pardinus*, *Mammuthus* sp., *E. altidens*, *S. hundsheimensis*, *H. antiquus*, *Sus* sp., *D. vallonnentensis*, *Me. savini*, *Bison* sp., Bovidae indet., Caprini indet., *M. savini*, *Iberomys huescarensis*, *Stenocranius gregaloides*, *Apodemus* cf. *sylvaticus*, *Eliomys quericinus*, and *Hystrix refossa*.

3. Results

3.1. Species abundance

The samples analyzed differ in their respective NISP (>2500 in layer EVT7, 325 in layer CGRD2) and number of recorded taxa (from 21 in EVT to 12 in both CGR2 and CGRD7) (Fig. 3). However, herbivore species are the most abundant in all the studied layers, with a huge proportion of hippos, which represent in the three samples >30% of total NISP values. Similarly, fallow deer-like cervids are in all instances the second most abundant species, with >15% of total NISP values (Fig. 3). Rhinos and horses are also well documented, with a mean close to 10% in the three layers. The remaining herbivore species (i.e., primates, proboscideans, bovids, suids and giant deer) are less represented, with percentages usually <5% (Fig. 3). Concerning the carnivores, layer EVT7 shows a high diversity with 10 identified taxa. Carnivores are always less represented than ungulates in the Vallparadís Section, with percentages of <5% except for ursids and hyaenids, which are moderately abundant. However, hyena coprolites are frequently preserved in the studied assemblages, especially in layer EVT7, from which >400 coprolites where recovered (Fig. 5E).

3.2. Comparison with other Early Pleistocene sites

The faunal composition of Vallparadís Estació Layer EVT7, which provided the largest fossil assemblage, was compared with those of other Early Pleistocene sites of Europe using a contingency table, developed following the statistical procedure described in Palmqvist et al. (2011), which allows testing of the null hypothesis of homogenous distribution of taxa among the localities compared. The results obtained in the contingency table (Table 1) show that compared to other Early Pleistocene sites, the faunal assemblage of Vallparadís Estació shows frequencies greater than expected from a random distribution for proboscideans, hippos and, to a lesser extent, other large mammal taxa, while the frequencies of bovids, cervids and perissodactyls are lower than expected in all cases.

Concerning proboscideans, Fuente Nueva-3 is the only other site that shows a particularly rich record of these animals. For hippos, the only other site that shows a frequency of this species higher than expected is Barranco León. The scarcity of bovids at Vallparadís Estació is similar to those of Barranco León and Fuente Nueva-3, while the comparatively low frequency of cervids compares to Fuente Nueva-3 and Venta Micena. However, the low frequency of perissodactyls is similar to the record of Untermassfeld in Central Europe, as these species are overrepresented in the faunal assemblages of the other three sites of the Iberian Peninsula compared (i.e., Barranco León, Fuente Nueva-3 and Venta Micena).

Given that perissodactyls are monogastric, hindgut-fermenting ungulates, while bovids and cervids are foregut-fermenting ruminants, the difference in abundance of perissodactyls between the three sites of the Guadix-Baza Basin and Untermassfeld could relate to differences in the quality and abundance of the plant resources available in Southern and Central Europe. Specifically, the digestive system of a hindgut fermenter relies on a rapid passage rate of the ingesta and the processing of large quantities of food, which allows them to consume low quality grasses too fibrous for a ruminant to subsist on. In contrast, ruminants are very efficient at extracting maximum amounts out of the cellulose and cell contents of food of moderate fiber content, and if feeding on vegetation of relatively good quality they can subsist on a lesser amount of food per day than a hindgut fermenter of similar size (see review in Palmqvist et al., 2008a). For this reason, the difference in abundance of perissodactyls between the studied sites probably reflects differences in the quality of the vegetation available. However, this explanation does not apply to Vallparadís Estació Layer EVT7, which climate and vegetation would be more similar to those of the Guadix-Baza Basin, which suggests that other factors biased the abundance of perissodactyls at this site.

Vallparadís Estació is the only site that shows a frequency of carnivores similar to that expected from a random distribution. In contrast, the three sites of the Guadix-Baza Basin show frequencies that are significantly lower than those expected, while Untermassfeld has an overrepresentation of these taxa. Given that two sites of the Guadix-Baza Basin, Barranco León and Fuente Nueva-3,

Table 1
Chi-squared contingency table for the distribution of *NISP* values among groups of large mammals in level EVT7 of Vallparadís and in a number of Early Pleistocene assemblages. In each cell, raw frequencies, expected frequencies (in brackets) and adjusted residuals (*t*-test values). $\chi^2 = 3746.0$ ($p < 0.001$). Probabilities for adjusted residuals (two-tailed): * $p < 0.05$, $t \geq 1.960$; ** $p < 0.01$, $t \geq 2.576$; *** $p < 0.001$, $t \geq 3.291$.

Taxa/site	Vallparadís EVT7	Untermassfeld	Venta Micena	Barranco León	Fuente Nueva-3	Σi
Proboscideans	103 (43.9) 8.202***	29 (73.7) −4.424***	51 (107.0) −4.149***	1 (14.0) −3.407***	74 (19.5) 11.987***	258
Hippopotamids	760 (231.0) 33.281***	320 (388.0) −3.050**	63 (563.0) −16.809***	158 (73.7) 10.022***	57 (102.4) −4.525***	1358
Bovids	153 (491.5) −15.513***	1058 (825.7) 7.592***	1448 (1198.1) 6.121***	106 (156.8) −4.397***	125 (217.9) −6.746***	2890
Cervids	492 (541.7) −2.197*	1302 (910.0) 12.358***	1065 (1320.4) −6.032***	163 (172.8) −0.818	163 (240.2) −5.404***	3185
Perissodactyls	707 (932.5) −8.490***	827 (1566.5) −19.850***	2971 (2273.0) 14.040***	337 (297.5) 2.811**	641 (413.5) 13.565***	5483
Carnivores	263 (247.3) 0.958	640 (415.4) 9.772***	490 (602.8) −3.677***	21 (78.9) −6.672***	40 (109.6) −6.731***	1454
Other taxa	30 (20.1) 2.028*	37 (33.7) 0.479	25 (48.9) −2.610**	14 (6.4) 2.931**	12 (8.9) 1.003	118
Σj	2508	4213	6113	800	1112	14,746

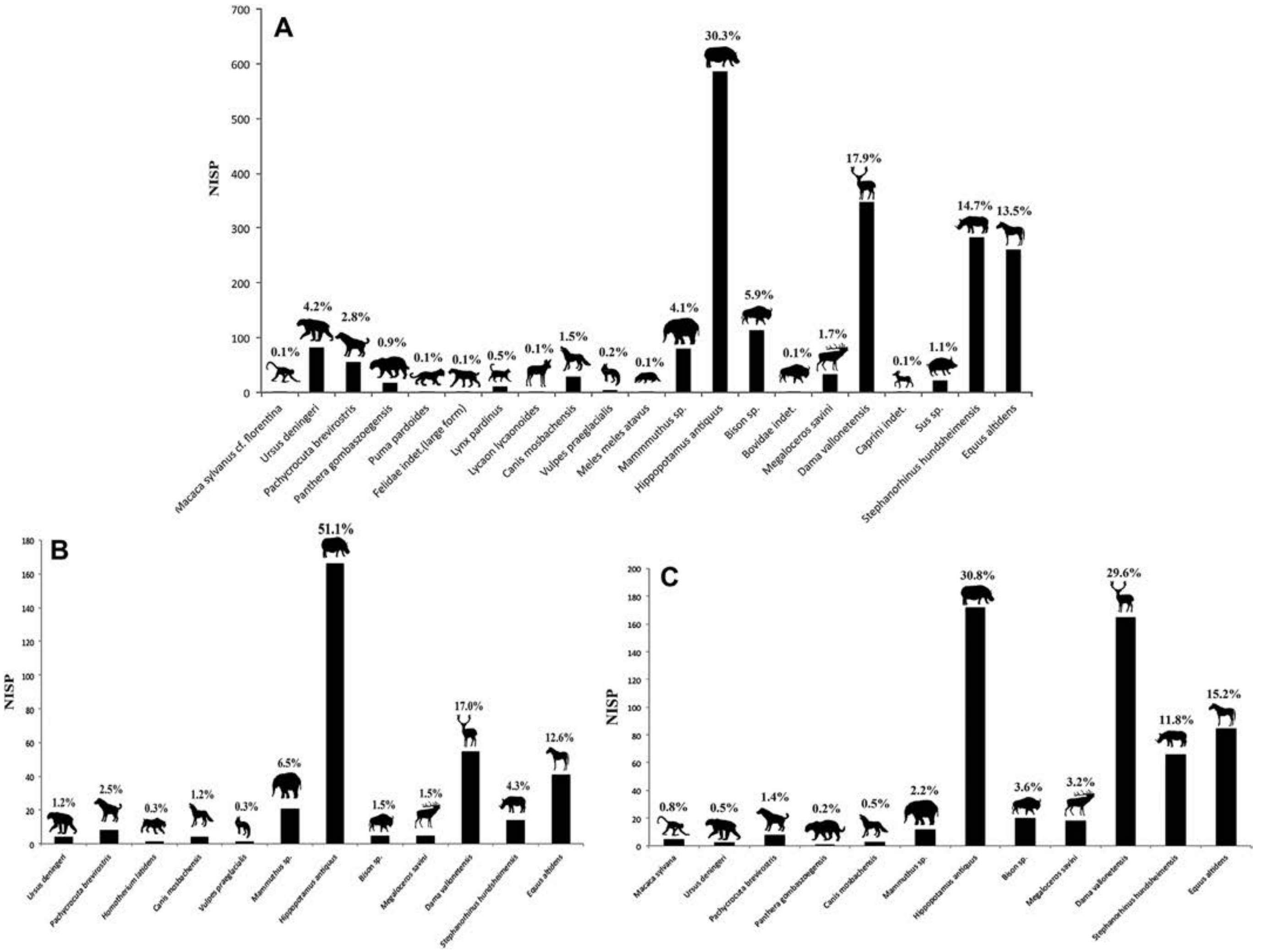

Fig. 3. Species abundances in number of identifiable specimens (NISP) in (A) layer EVT7, (B) layer CGRD2 and (C) layer CGRD7.

have provided evidence of human presence, including the finding of huge Oldowan tool assemblages and cut marks on the skeletal remains of ungulates, this could relate to the ecological displacement of scavenging carnivores by the hominins at these sites.

3.3. Distribution of skeletal specimens

A total of 4304 remains were prepared and studied, of which 3421 (79.4%) can be identified both anatomically and taxonomically. This high percentage of identifiable remains is a consequence of the large amount of material pending preparation, which mostly consists of small fragments and fractured diaphyses. According to the obtained data, isolated teeth are in all layers the most abundant elements, representing >20% in CGRD2 and close to 40% in EVT7 and CGRD7. Concerning the other analyzed categories, there is a high degree of variation. For example, several hippo skeletons where recovered in semianatomical connection from layer CGRD2, whose origin has been related with debris flow events. For this reason, there is a high percentage of vertebrae/ribs (21.7%) and autopodial bones (23.9%) in this layer (Fig. 4B). In contrast, layer EVT7, which has been related with mud-flow events, only provided two skeletons in semianatomical connection (corresponding to one specimen of *H. antiquus* and another of *P. brevirostris*), thus displaying a higher frequency of major limb bones (21.5%) and a lower proportion of both vertebrae/ribs (9.3%) and autopodial bones (11.9%; Fig. 4A). Layer CGRD7 shows a completely different pattern, because in spite of a similar prevalence of isolated teeth (39%), vertebrae/ribs (14.6%), long bones (14.2) and autopodial bones (20.3%) are less common and show a similar abundance (Fig. 4C).

3.4. Conservation, abundance of epiphyses and major long bones

The bones studied do not show evidence of a high degree of weathering. Most bones group in the weathering stage 1 of Behrensmeyer (1978), which suggests a period of less than three years of subaerial exposure before their definitive burial in the sediment. However, complete bones are rare in layers CGRD2, CGRD7 and EVT7, and those preserved as almost complete generally correspond either to compact bones (such as carpals, tarsals and phalanges, which usually show gnaw marks; Fig. 5H), isolated teeth or, in the case of layer CGRD2, complete vertebrae and ribs from the hippo partial skeletons (Fig. 4). The fragmentary bones recovered mostly correspond to partial long bones with gnawed or absent epiphyses, fragmentary mandibular corpora, maxillary fragments, and partial antlers of fallow deer-cervids (which preserve part of the frontal and the pedicle; Fig. 5A–C,F).

The recovered bones of herbivores mainly correspond to very large-bodied species, 3b and 4 size classes following Brain (1981) and Bunn (1982), such as hippos, horses, rhinos, large bovids, and cervids. There are abundant identifiable skeletal elements of the

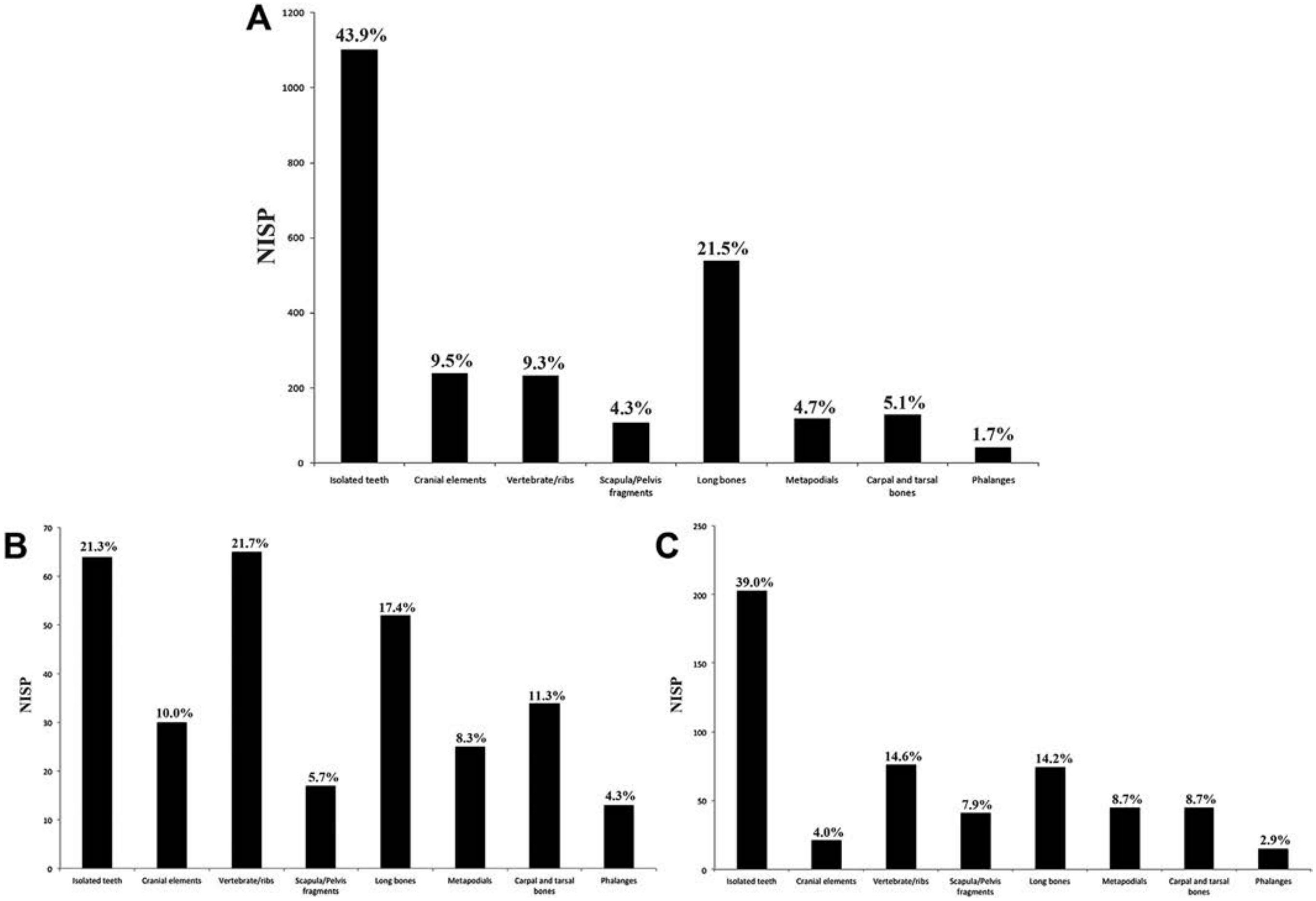

Fig. 4. Distribution of skeletal specimens in (A) layer EVT7, (B) layer CGRD2 and (C) layer CGRD7.

medium-sized fallow deer-like *D. vallonnetensis* (Fig. 3), although they mainly correspond to fragmentary mandibular corpora or maxillae, as well as antler fragments (Fig. 5F,J). Almost no identifiable postcranial bones of *D. vallonnetensis* were recovered, and the few available correspond to very fragmentary diaphyses, probably related to the abundance of coprolites in all the studied layers.

The largest sample available (layer EVT7, NISP > 2500) was used to test for differences of preservation between major long bones and autopodial bones (Table 2). We compared the preservation of these bone categories in the most abundant species of this layer (the hippo *H. antiquus*), by considering five different categories: complete bones, diaphyses, fragments of distal epiphyses, fragments of proximal epiphyses and diaphyseal fragments (Table 2). Our results show that most long bones are preserved as distal fragments and partial diaphyses, and that only the radius-ulna is well represented by proximal fragments, although most of them correspond to fragments of the oleocranon process. In contrast, complete bones mainly correspond to metapodials, carpals, tarsals and phalanges (Table 2). The same analysis was performed including the remains of the appendicular skeleton from all large herbivores documented in EVT7: *H. antiquus*, *S. hundsheimensis*, *E. altidens*, *Me. savini* and *Bison* sp. This second analysis provided virtually the same results of the first one (Table 2).

Table 2
Pattern of breakage for different skeletal specimens of large mammals recovered from layer EVT7. Large herbivores include: *Hippopotamus*, *Stephanorhinus*, *Equus*, *Bison* and *Megaloceros*. Mtc, Metacarpal; Mtt: Metatarsal.

	Humerus	Radius-ulna	Femur	Tibia	Carpal/tarsal	Mtc/Mtt	Phalanges	
Hippopotamus								
Complete	4	7	3	1	26	10	2	**53**
Diaphisys	5	0	19	2	0	0	0	**26**
Distal frag.	9	0	0	12	0	0	0	**21**
Proximal frag.	0	15	8	0	0	1	0	**24**
Fragment	0	1	4	0	10	1	2	**18**
	18	**23**	**34**	**15**	**36**	**12**	**4**	
Large herbivores								
Complete	4	16	3	6	49	49	11	**138**
Diaphisys	5	3	30	3	0	1	0	**42**
Distal frag.	23	4	3	33	0	7	2	**72**
Proximal frag.	1	34	8	0	0	7	2	**52**
Fragment	0	3	2	0	16	0	0	**21**
	33	**60**	**46**	**42**	**65**	**64**	**15**	

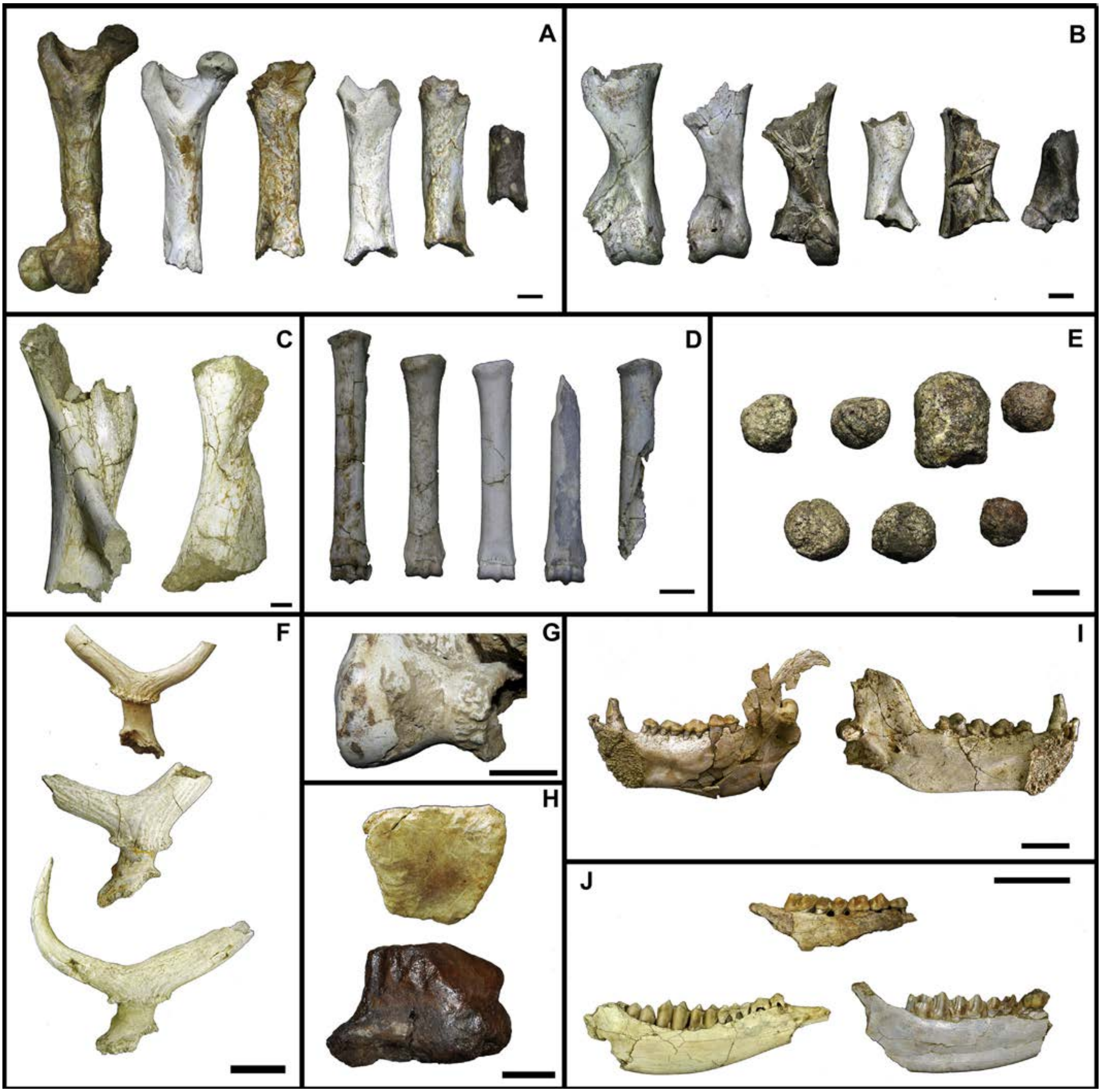

Fig. 5. Large mammal remains from the Vallparadís Section. (A) Femora of *Hippopotamus antiquus* from EVT7. (B) Humerus of *H. antiquus* from EVT7. (C) Humerus of *Mammuthus* sp. from EVT7. (D) Metacarpals of *Equus altidens* from EVT7. (E) Coprolites of *Pachycrocuta brevirostris* from EVT7. (F) Partial antlers of *Dama vallonnetensis* from CGRD5, EVT7 and EVT12. (G) Detail of a distal epiphysis of femur of *H. antiquus* with gnaw-marks from EVT7. (H) Carpals of *Mammuthus* sp. with gnaw-marks from CGRD5 and CGRD2. (I) Two hemimandibles of *P. brevirostris* from EVT7 and EVT12. (J) Mandibular corpora of *D. vallonnetensis* from EVT7 and EVT12.

Carnivore damage has been identified on several ungulate remains. Modifications are located mainly on long bones of the appendicular skeleton. Pits and scores are the most abundant types of alteration on the faunal record, being present in both the distal and proximal epiphyses as well as in the diaphyses. Furrowing is also present in some distal epiphyses (Figs. 5G,H and 6B–D). In addition, analysis of bone breakage (Villa and Mahieu, 1991) shows that curved fractures with oblique angles and smooth edges predominate, which is indicative of fresh bone breakage (Fig. 6A).

4. Discussion

4.1. Biochronology and paleobiology of *Pachycrocuta brevirostris*

The earliest occurrence in Europe of the African origin giant hyena *P. brevirostris* corresponds to the Olivola faunal unit in Italy (ca 1.99 Ma; Palmqvist et al., 2011, and references therein). Its arrival into the continent was described as the “*P. brevirostris* event” by Martínez-Navarro (2010). Since its first record, this hyaenid

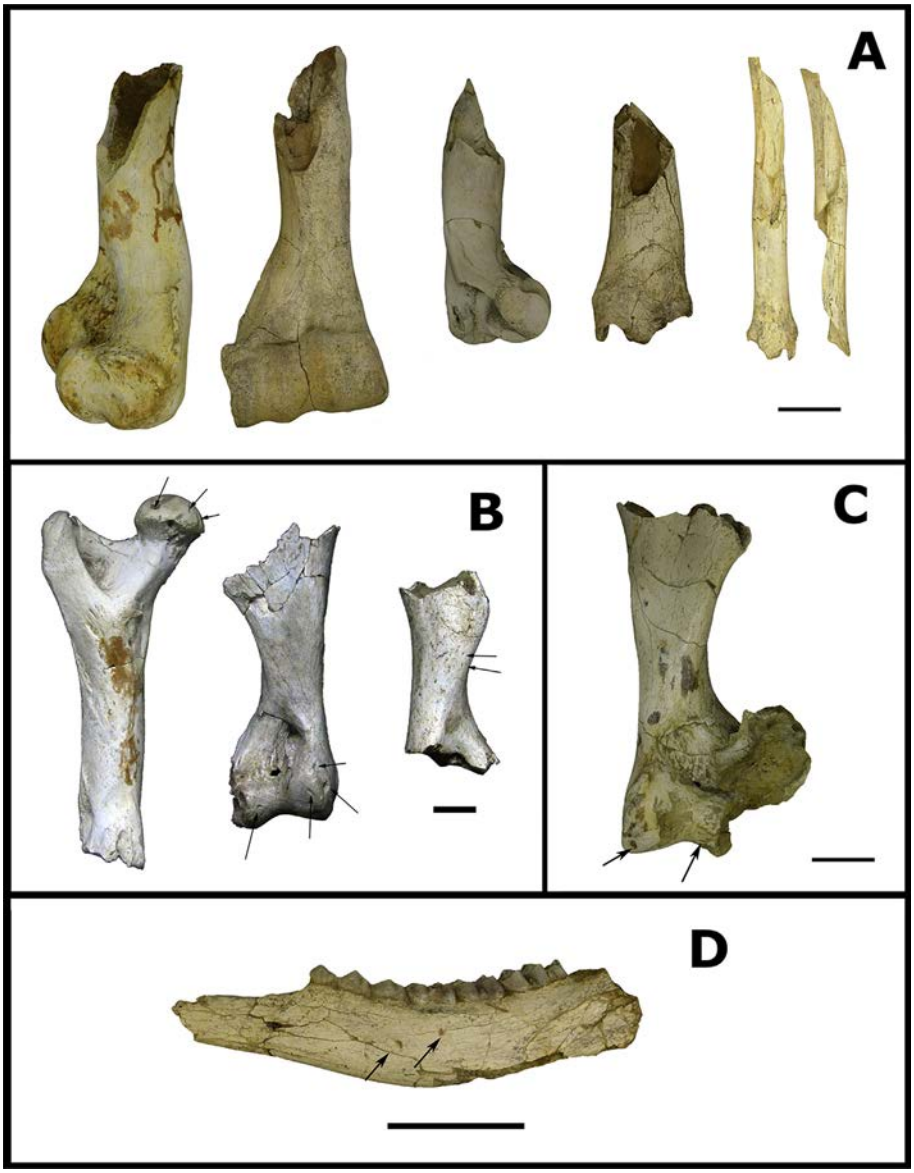

Fig. 6. Large mammal remains from the Vallparadís Section. (A) Long bones of *Equus altidens* and *Dama vallonnetensis* from EVT7 with typical fractures produced in fresh state. (B) Femur and (C) humerus of *Hippopotamus antiquus* from EVT7 with scores, pits and furrowing produced by *Pachycrocuta brevirostris* (B is a detail from Fig. 4B). (D) Mandible of *Dama vallonnetensis* from EVT7 with tooth pits.

became an ubiquitous species among the late Villafranchian and Epivillafranchian large mammal assemblages of Western Europe, its remains being recorded from a high number of sites, including Pirro Nord (ca. 1.6–1.3, Italy), Venta Micena (1.5 Ma, Spain), Barranco León and Fuente Nueva-3 (ca. 1.4–1.3 Ma, Spain), Incarcal I and V (1.4–1.3 Ma, Spain), Le Vallonnet (ca. 1.0 Ma, France) and Untermassfeld (ca. 1.0, Germany), among others (Turner et al., 2008; Palmqvist et al., 2011 and references therein). The well-calibrated last appearance of this species is precisely layer EVT7 of the Vallparadís Section (Fig. 5I; ca. 0.86 Ma; Madurell-Malapeira et al., 2010; Duval et al., 2015).

In spite of its large size (>100 kg; Palmqvist et al., 2011), *P. brevirostris* differs from the extant hyenas in the shortness of the distal limb bones (i.e., radius and tibia) relative to the proximal ones (i.e., humerus and femur). This presumably indicates a less cursorial life style for this species compared to the living hyenas, although it provided greater power and more stability for dismembering and carrying large pieces of ungulate carcasses (Turner and Antón, 1996). This fact suggests a strictly scavenging behavior for this species, which is in agreement with the taphonomic studies carried out at the site of Venta Micena (Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001; Espigares, 2010; Palmqvist et al., 2011).

4.2. *Known taphonomic evidences of the activity of Pachycrocuta brevirostris*

The research conducted in Venta Micena showed that *P. brevirostris* was the biotic agent responsible of accumulating and modifying most of the huge large mammal assemblage unearthed from this site (Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001; Espigares, 2010; Palmqvist et al., 2011). The results obtained showed that the bone-cracking activity of this large hyaenid is associated with the presence of robust mandibular corpora of ungulates preserved without the ramus as well as wide maxillary fragments preserved in isolation from the neurocranium. Cervid antlers are also normally preserved in an intensely fractured state, merely preserving part of the pedicle and a fragment of the frontal bone. Regarding the postcranial bones, a well-documented proximodistal sequence of consumption by for the humerus and tibia, an inverse sequence of modification for the radius, and a less clearly defined pattern of consumption for the femur have been documented for this hyaenid (Espigares, 2010; Palmqvist et al., 2011). In particular, the very low numbers of complete tibiae and humeri preserved, as well as the abundance of femoral diaphyses, can be related to the higher grease content of these bones. To sum up, the results from Venta Micena suggest a selective bone crushing behavior for *P. brevirostris*, with important differences in the patterns of limb bone consumption being putatively related to the respective position of each bone within the skeleton, as well as to their mineral densities, fat contents and nutritional value (Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001; Palmqvist et al., 2011). Such behavior has been also recently documented in the sites of Barranco León and Fuente Nueva-3 (Espigares, 2010; Espigares et al., 2013).

4.3. Inferences on the Vallparadís Section

All the layers studied are associated with high-density catastrophic flows (debris and mud flows). The bias caused by more or less prolonged transport is not well resolved yet. The preservation state of the recovered bones (which include large cervid antlers and hippo bones) suggests a minor influence of water transportation and sorting in the taphocenoses.

Concerning the species composition and their paleoecological implications, the presence of abundant remains of *H. antiquus* in these layers (>30% of the total preserved remains in all instances; Fig. 3) is indicative of warm and humid conditions, as the extinct *H. antiquus* (closely related to the extant *Hippopotamus amphibius*) is unlikely to have tolerated very cold temperatures (leading to the seasonal freezing of the rivers they inhabited; Madurell-Malapeira et al., 2010; García-Aguilar et al., 2014, 2015). Moreover, this hippo species was more dependent of the aquatic environments than *H. amphibious*, as suggested by its huge size (3200 kg average mass) and shortened metapodials, as well as by biogeochemical analysis of bone collagen isotopes in Venta Micena, which show that *H. antiquus* fed on aquatic macrophytes instead of grazing on terrestrial grasses, as do the living hippos (Palmqvist et al., 2003, 2008a, 2008b; García-Aguilar et al., 2014, 2015). This suggests that *H. antiquus* could not have inhabited watercourses that froze in winter or desiccated in summer. The presence of warm and humid conditions at Vallparadís is further indicated by the abundance of large mammal species with preference for open habitats (such as savanna-like environments with sparse woodlands), including the browsers *D. vallonnetensis* and *S. hundsheimensis*, as well as the grazer *E. altidens* (Fig. 3). However, macromammal species with preference for more wooded habitats with abundant water in their vicinity, such as *P. gombaszoegensis* and *M. sylvanus* cf. *florentina*, are more scarcely represented, but it should be taken into account that carnivorans and primates generally display lower population densities than ungulates, thus being less common among fossil thaphocoenoses.

The virtually exclusive record of very large-bodied species (Fig. 3) and the abundance of coprolites suggest, based on this preliminary study, a bias produced by the bone-cracking hyena *P. brevirostris*. A predominance of hippo, horse, rhino and medium-sized deer remains has been also recorded in other open-air European sites of similar chronology, such as the Orce sites in Spain (Arribas and Palmqvist, 1998; Espigares, 2010), Colle Curti in Italy (Mazza and Ventra, 2011), and particularly Untermassfeld in Germany (Kahlke, 2006).

The distribution of skeletal specimens, clearly different among the studied layers, is marked by the preponderance of isolated teeth (Fig. 4). This can be related with diagenetic processes, which would produce differential preservation according to the composition and degree of mineralization of the skeletal remains, as documented in Venta Micena, Barranco León and Fuente Nueva-3 (Espigares, 2010; Espigares et al., 2013).

The documented patterns of preservation, as reflected in the abundance of epiphyses and major long bones, especially in EVT7, resemble those from other sites such as Venta Micena (Table 2; Palmqvist et al., 2011). As for the latter site, our results suggest a selective bone crushing behavior by *P. brevirostris*, with important differences in the patterns of consumption of various limb bones, which may be presumably related to their position in the skeleton, on the one hand, and their fat content and nutritional value, on the other. In the studied layers, maxillae and mandibles are usually broken, with the latter being preserved without the ramus and with the corpus fragmented (Fig. 5J). Antlers are usually preserved as fragments, often associated with part of the frontal bone (Fig. 5F). The long bones tend to be preserved as distal fragments in the case of the humerus and tibia, as diaphyses in the case of the femur, and as distal fragments in the case of metapodials (Fig. 5A–D). In contrast, the carpals, tarsals and phalanges are usually preserved complete (Table 2; Fig. 5H).

4.4. Implications for hominin dispersals and survival

The climatic shifts associated with the Mid-Pleistocene Revolution and the competition with Villafranchian carnivores were likely limiting factors for the survival of the first European hominins. On the one side, the survival of most of the late Villafranchian ungulates and carnivorans at least until 0.86 Ma (layer EVT7) and the predominance of hippo remains in the different layers of the Vallparadís Section during the Mid-Pleistocene Revolution suggest that the effects of these climatic shifts in the large mammal assemblages (including hominins) were less than expected for the Mediterranean Europe (Madurell-Malapeira et al., 2010). The only differences between the late Villafranchian and the Epivillafranchian large mammal assemblages are the dispersal into Europe of suids of the *Sus scrofa* lineage as well as the replacement of two species of cervids (*Praemegaceros verticornis* by *M. savini* and *Metacervocerus rhenanus* by *D. vallonnetensis*). These Epillafranchian suids and cervids are recorded in several sites of this age, such as Sima del Elefante TD9, Vallparadís Section, Vallonnet, Cueva Victoria, Untermassfeld and Bòvila Ordis (Moullé, 1992; Kahlke, 2006; Carbonell et al., 2008; Madurell-Malapeira et al., 2014; J. M.-M., unpublished data). The latter assumption is reinforced by recent studies on Iberian and Italian Peninsulas, which suggest that the Mid-Pleistocene Revolution did not imply marked changes in the vegetation cover (e.g., Suc and Popescu, 2005; Magri and Palombo, 2013).

The evidence reported here shows that the carnivore guild, the open environments and the good climatic conditions of the late Villafranchian apparently remained stable in Iberian at least until the Epivillafranchian (i.e., from ca. 1.8 to 0.8 Ma). Food acquisition must have been one of the key problems for the first human populations of temperate Europe, where meat and fat consumption during the winter was a major limiting factor (Martínez-Navarro, 2010; Martínez-Navarro et al., 2014). This probably induced hominins to develop scavenging strategies focused on ungulate carcasses (Martínez-Navarro and Palmqvist, 1995, 1996; Arribas and Palmqvist, 1998; Palombo, 2014). The availability of these carcasses depended to a large extent on the internal structure of the carnivore guild, especially on the interrelationships among the top predators. In particular, it has been suggested that the presence of stable populations of saber-toothed felids in the late Early Pleistocene of Europe, and particularly the activity of the dirk-toothed cat *Meganteron whitei*, probably opened an ecological niche for scavengers (Martínez-Navarro and Palmqvist, 1995, 1996). This niche was probably occupied by both *Pachycrocuta* and early *Homo*, as *Megantereon*, given its great killing capabilities and highly derived dental characteristics, was probably unable to consume all of the meat that it obtained by hunting large ungulates (Turner, 1992; Martínez-Navarro and Palmqvist, 1995, 1996; Palmqvist et al., 1996, 2005, 2007). Therefore, these early human populations likely competed for these carcasses directly with very powerful carnivorans (such as saber-toothed felids, *Pachycrocuta* and, probably, pack hunting lycaons, the jaguar *P. gombaszoegensis*, the giant cheetah *Acinonyx pardinensis* and the puma-like cat *P. pardoides*, among others) by means of confrontational scavenging.

On the other hand, the preliminary taphonomic evidence reported in this paper suggests an active role of *P. brevirostris* in the studied layers of the Vallparadís Section, which further reinforces the ideas exposed above. The carnivore guild remained stable during all the Late Villafranchian and Epivillafranchian and the activity of *P. brevirostris* was probably a persisting limiting factor for hominin food acquisition throughout all the late Early Pleistocene (ca. 1.4–0.8 Ma).

5. Conclusions

The earliest occurrence of hominins in Western Europe is recorded in three Iberian sites: Barranco León, Fuente Nueva-3 and Sima del Elefante TD9. During the Late Villafranchian, as exemplified in the Orce sites, the climatic conditions remained stable and the existing open environments probably favored the dispersal of early *Homo* into the Mediterranean Europe. However, the presence of large predators, such as saber-toothed felids and the giant hyaenid *P. brevirostris*, was probably a limiting factor for food acquisition for these hominins. Later on, during the Epivillafranchian, the climatic conditions became unstable as a consequence of the climatic shifts associated to the Mid-Pleistocene Revolution. Some scholars have suggested that such unfavorable climatic conditions probably conditioned the subsistence of these early hominins. However, the evidence reported in this paper suggests that both climatic conditions and large mammal assemblages, at least in Iberia, remained stable during the Epivillafranchian. In particular, the evidence provided here from the Vallparadís Section record indicates that the composition of the carnivore guild as well as the role of *P. brevirostris* (as a bone accumulator and competitor for hominins in the access to ungulate carcasses left by sabertooths) apparently remained unchanged throughout the late Villafranchian and Epivillafranchian.

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References

Arribas, A., Palmqvist, P., 1998. Taphonomy and palaeoecology of an assemblage of large mammals: hyaenid activity in the Lower Pleistocene site at Venta Micena (Orce, Guadix-Baza Basin, Granada, Spain). Geobios 31, S3–S47.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology 4, 150–162.

Berástegui, X., Casanovas, J., Moyà, S., 2000. El jaciment paleontològic de Cal Guardiola. Una finestra oberta al Plistocè Inferior de Catalunya. Contextualització geològica. Tribuna d'Arqueologia 1997–1998, 255–277.

Berástegui, X., Losantos, M., 2001. Mapa geològic de Catalunya a escala 1:25000 (Sabadell).

Boscaini, A., 2014. Plio-Pleistocene Lynxes from the Iberian Peninsula. Taxonomy and Phylogenetic Relationships with the Extant and Fossil Species (Master thesis). Universitat Autònoma de Barcelona and Universitat de Barcelona.

Brain, C.K., 1981. The Hunters or the Hunted? An Introduction to African Cave Taphonomy. The University of Chicago Press, p. 365.

Bunn, H.T., 1982. Meat-eating and Human Evolution: Studies on the Diet and Subsistence Patterns of Plio-Pleistocene Hominids in East Africa (Ph.D. dissertation). University of California Berkeley.

Carbonell, E., Bermúdez De Castro, J.M., Parés, J.M., Pérez-González, A., Cuenca-Bescós, G., Ollé, A., Mosquera, M., Huguet, R., van der, Made J., Rosas, A., Sala, R., Vallverdú, J., García, N., Granger, D.E., Martinón-Torres, M., Rodríguez, X.P., Stock, G.M., Vergés, J.M., Allué, E., Burjachs, F., Cáceres, I., Canals, A., Benito, A., Díez, C., Lozano, M., Mateos, A., Navazo, M., Rodríguez, J., Rosell, J., Arsuaga, J.L., 2008. The first hominin of Europe. Nature 452, 465–469.

Clark, P., Archer, D., Pollard, D., Blum, J.D., Rial, J.A., Brovkin, V., Mix, A.C., Pisias, N.G., Roy, M., 2006. The Middle Pleistocene transition: characteristics, mechanisms, and implications for long-term changes in atmospheric pCO_2. Quaternary Science Reviews 25, 3150–3184.

Duval, M., Bahain, J.J., Falguères, C., Garcia, J., Guilarte, V., Grün, R., Martínez, K., Moreno, D., Shao, Q., Voinchet, P., 2015. Revisiting the ESR chronology of the Early Pleistocene hominin occupation at Vallparadís (Barcelona, Spain). Quaternary International 389, 213–223.

Espigares, M.P., 2010. Análisis y Modelización del Contexto Sedimentario y los Atributos Tafonómicos de los Yacimientos Pleistocénicos del borde Nororiental de la Cuenca de Guadix-Baza (Ph.D. dissertation). Universidad de Granada, Granada.

Espigares, M.P., Martínez-Navarro, B., Palmqvist, P., Ros-Montoya, S., Toro, I., Agustí, J., Sala, R., 2013. *Homo* vs. *Pachycrocuta*: earliest evidence of competition for an elephant carcass between scavengers at Fuente Nueva-3 (Orce, Spain). Quaternary International 295, 113–125.

García-Aguilar, J.M., Guerra-Merchán, A., Serrano, F., Palmqvist, P., Flores-Moya, A., Martínez-Navarro, B., 2014. Hydrothermal activity and its paleoecological implications in the latest Miocene to Middle Pleistocene lacustrine environments of the Baza Basin (Betic Cordillera, SE Spain). Quaternary Science Reviews 96, 204–221.

García-Aguilar, J.M., Guerra-Merchán, A., Serrano, F., Flores-Moya, A., Delgado-Huertas, A., Espigares, M.P., Ros-Montoya, S., Martínez-Navarro, B., Palmqvist, P., 2015. A reassessment of the evidence for hydrothermal activity in the Neogene-Quaternary lacustrine environments of the Baza basin (Betic Cordillera, SE Spain) and its paleoecological implications. Quaternary Science Reviews 112, 226–235.

Kahlke, R.-D., 2006. Untermassfeld: a Late Early Pleistocene (Epivillafranchian) Fossil Site Near Meiningen (Thuringia, Germany) and its Position in the Development of the European Mammal Fauna, vol. 1578. British Archaeological Reports Ltd.

Leroy, S.A.G., Arpe, K., Mikolajewicz, U., 2011. Vegetation context and climatic limits of the Early Pleistocene hominin dispersal in Europe. Quaternary Science Reviews 30, 1448–1463.

Magri, D., Palombo, M.R., 2013. Early to Middle Pleistocene dynamics of plant and mammal communities in South West Europe. Quaternary International 288, 63–72.

Madurell-Malapeira, J., Minwer-Barakat, R., Alba, D.M., Garcés, M., Gómez, M., Aurell-Garrido, J., Ros-Montoya, S., Moyà-Solà, S., Berástegui, X., 2010. The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe. Quaternary Science Reviews 29, 2972–2982.

Madurell-Malapeira, J., Ros-Montoya, S., Espigares, M.P., Alba, D.M., Aurell-Garrido, J., 2014. Villafranchian large mammals from the Iberian Peninsula: paleobiogeography, paleoecology and dispersal events. Journal of Iberian Geology 40, 167–178.

Martínez-Navarro, B., 2010. Early Pleistocene faunas of Eurasia and hominid dispersals. In: Fleagle, J.G., Shea, J.J., Grine, F.E., Baden, A.L., Leakey, R.E. (Eds.), The First Hominin Colonization of Eurasia, Contribution from the Second Stony Brook Human Evolution Symposium and Workshop, vol. 13. Springer, pp. 207–224.

Martínez-Navarro, B., Palmqvist, P., 1995. Presence of the African machairodont *Megantereon whitei* (Broom 1937) (Felidae, Carnivora, Mammalia) in the Lower Pleistocene site of Venta Micena (Orce, Granada, Spain), with some considerations on the origin, evolution and dispersal of the genus. Journal of Archaeological Science 22, 569–582.

Martínez-Navarro, B., Palmqvist, P., 1996. Presence of the African saber-toothed felid *Megantereon whitei* (Broom, 1937) (Mammalia, Carnivora, Machairodontinae) in Apollonia-1 (Mygdonia Basin, Macedonia, Greece). Journal of Archaeological Science 23, 869–872.

Martínez-Navarro, B., Turq, A., Agustí, J., Oms, O., 1997. Fuente Nueva-3 (Orce, Granada, Spain) and the first human occupation of Europe. Journal of Human Evolution 133, 611–620.

Martínez-Navarro, B., Espigares, M.P., Pastó, I., Ros-Montoya, S., Palmqvist, P., 2014. Early *Homo* fossil records of Europe. In: Smith, C. (Ed.), Encyclopedia of Global Archaeology, pp. 2561–2570.

Mazza, P.P.A., Ventra, D., 2011. Pleistocene debris-flow deposition of the hippopotamus-bearing Collecurti bonebed (Macerata, Central Italy): taphonomic and paleoenvironmental analysis. Palaeogeography Palaeoclimatology Palaeoecology 310, 296–314.

Mendoza, M., Janis, C.M., Palmqvist, P., 2005. Ecological patterns in the trophic-size structure of large mammal communities: a 'taxon-free' characterization. Evolutionary Ecological Research 7, 505–530.

Minwer-Barakat, R., Madurell-Malapeira, J., Alba, D.M., Aurell-Garrido, J., De Esteban-Trivigno, S., Moyà-Solà, S., 2011. Pleistocene rodents from the torrent de Vallparadís section (Terrassa, northeastern Spain) and biochronological implications. Journal of Vertebrate Paleontology 31, 849–865.

Moullé, P.E., 1992. Les Grands Mammifères du Pléistocene Inférieur de la grotte du Vallonnet (Roquebrune-Cap-Martín, Alpes Maritimes). Étude paléontologique des Carnivores, Equidé, Suidé et Bovidés (Ph.D. dissertation). Muséum National d'Histoire Naturelle, Paris.

Palmqvist, P., Arribas, A., 2001. Taphonomic decoding of the paleobiological information locked in a lower Pleistocene assemblage of large mammals. Paleobiology 27, 512–530.

Palmqvist, P., Martínez-Navarro, B., Arribas, A., 1996. Prey selection by terrestrial carnivores in a Lower Pleistocene paleocommunity. Paleobiology 22, 514–534.

Palmqvist, P., Gröcke, D.R., Arribas, A., Fariña, R., 2003. Paleoecological reconstruction of a lower Pleistocene large mammals community using biogeochemical ($\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$, Sr:Zn) and ecomorphological approaches. Paleobiology 29, 205–229.

Palmqvist, P., Martínez-Navarro, B., Toro, I., Espigares, M.P., Ros-Montoya, S., Torregrosa, V., Pérez-Claros, J.A., 2005. A re-evaluation of the evidence of human presence during Early Pleistocene times in southeastern Spain. L'Anthropologie 109, 411–450.

Palmqvist, P., Torregrosa, V., Pérez-Claros, J.A., Martínez-Navarro, B., Turner, A., 2007. A re-evaluation of the diversity of *Megantereon* (Mammalia, Carnivora, Machairodontinae) and the problem of species identification in extinct carnivores. Journal of Vertebrate Paleontology 27, 160–175.

Palmqvist, P., Pérez-Claros, J.A., Gröcke, D.R., Janis, C.M., 2008a. Tracing the ecophysiology of ungulates and predator-prey relationships in an early Pleistocene large mammal community. Palaeogeography Palaeoclimatology Palaeoecology 266, 95–111.

Palmqvist, P., Pérez-Claros, J.A., Janis, C.M., Figueirido, B., Torregrosa, V., Gröcke, D.R., 2008b. Biogeochemical and ecomorphological inferences on prey selection and resource partitioning among mammalian carnivores in an early Pleistocene community. Palaios 23, 724–737.

Palmqvist, P., Martínez-Navarro, B., Pérez-Claros, J.A., Torregrosa, V., Figueirido, B., Jiménez-Arenas, J.M., Espigares, M.P., Ros-Montoya, S., De Renzi, M., 2011. The giant hyena *Pachycrocuta brevirostris*: modeling the bone-cracking behavior of an extinct carnivore. Quaternary International 243, 61–79.

Palombo, M.R., 2014. Desconstructing mammal dispersals and faunal dynamics in SW Europe during the Quaternary. Quaternary Science Reviews 96, 50–71.

Rodríguez, J., Rodríguez-Gómez, G., Martín-González, J.A., Goikoetxea, I., Mateos, A., 2012. Predator–prey relationships and the role of *Homo* in Early Pleistocene food webs in Southern Europe. Palaeogeography, Palaeoclimatology and Palaeoecology 365, 99–114.

Rodríguez-Gómez, G., Rodríguez, J., Martín-González, J.Á., Goikoetxea, I., Mateos, A., 2013. Modeling trophic resource availability for the first human settlers of Europe: the case of Atapuerca TD6. Journal of Human Evolution 64, 645–657.

Suc, J.P., Popescu, S.M., 2005. Pollen records and climatic cycles in the North Mediterranean region since 2.7 Ma. In: Head, M.J., Gibbard, E.L. (Eds.), Early-Middle Pleistocene Transitions: the Land-ocean Evidence. Geological Society, London, Special Publication 247, pp. 147–158.

Toro-Moyano, I., Martínez-Navarro, B., Agustí, J., Souday, C., Bermúdez de Castro, J.M., Martinón-Torres, M., Fajardo, B., Duval, M., Falguères, C., Oms, O., Parés, J.M., Anadón, P., Julià, R., García-Aguilar, J.M., Moigne, A.-M., Espigares, M.P., Ros-Montoya, S., Palmqvist, P., 2013. The oldest human fossil in Europe, from Orce (Spain). Journal of Human Evolution 65, 1–9.

Turner, A., 1992. Large carnivores and earliest European hominids: changing determinants of resource availability during the Lower and Middle Pleistocene. Journal of Human Evolution 22, 109–126.

Turner, A., Antón, M., 1996. The giant hyena, *Pachycrocuta brevirostris* (Mammalia, Carnivora, Hyaenidae). Geobios 29, 455–468.

Turner, A., Antón, M., 1998. Climate and evolution: implications of some extinction patterns in African and European machairodontine cats of the Plio-Pleistocene. Estudios Geológicos 54, 209–230.

Turner, A., Antón, M., Werdelin, L., 2008. Taxonomy and evolutionary patterns in the fossil Hyaenidae of Europe. Geobios 41, 677–687.

Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. Journal of Human Evolution 21, 27–48.

Chapter 8. On the original author and year of description of the extinct hyaenid *Pachycrocuta brevirostris*.

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Summary: This nomenclatural work clarifies the taxonomic authority (original authorship) of the extinct hyaenid *Pachycrocuta brevirostris*.

Author's contribution: The doctoral candidate is the second author of this work. He was directly involved in all the stages of its development, from its initial design to bibliographic search and elaborating the conclusions, and revised the whole manuscript.

Brief report *Acta Palaeontologica Polonica* 60 (3): 573–576, 2015

On the original author and year of description of the extinct hyaenid *Pachycrocuta brevirostris*

DAVID M. ALBA, VÍCTOR VINUESA, and JOAN MADURELL-MALAPEIRA

The International Code of Zoological Nomenclature recommends providing the author and year of original description of any taxon, when first mentioned in a publication, which is useful for both taxonomic and nomenclatural reasons. Here we show that the authorship of the extinct hyaenid taxon *Hyaena brevirostris*, type species of the genus *Pachycrocuta*, has been incorrectly attributed to "Aymard, 1846" for more than a century on the basis of a publication that never existed. Our bibliographic research indicates that the first published work in which the name was employed—Gervais' (1848–1852) *Zoologie et Paléontologie françaises*, the part dealing with carnivorans being issued in 1850—fulfils the criteria of availability. Given that Gervais did not attribute the description to Aymard, but merely employed the latter's name in reference to a museum label/record (which does not constitute a valid indication), the correct name with authorship for this taxon is *Pachycrocuta brevirostris* (Gervais, 1850).

Introduction

The giant short-faced hyena, *Pachycrocuta brevirostris*—type species of genus *Pachycrocuta* Kretzoi, 1938—is a widespread extinct hyaenid, customarily classified in the bone-cracking ecomorphotype due to the possession of craniodental adaptations for breaking bones (Turner et al. 2008; Palmqvist et al. 2011) and further characterized by shortened distal limb segments—suggesting a body type well suited to dismembering and carrying large portions of ungulate carcasses (Palmqvist et al. 2011). With an estimated body mass of more than 110 kg, *P. brevirostris* is likely to have been the largest hyena that ever existed (Turner and Antón 1996; Palmqvist et al. 2011). It is first recorded in the Pliocene of both East Africa and Asia, ca. 3.0 Ma onwards (Werdelin and Solounias 1991; Werdelin and Lewis 2005; Palmqvist et al. 2011). In Europe its earliest appearance is not documented until later, ca. 2.0 Ma (Napoleone at al. 2003). The record of *P. brevirostris* extends to the Plio-Pleistocene boundary (2.6 Ma) in East Africa and until the middle Pleistocene (ca. 0.4 Ma) in Asia (Palmqvist et al. 2011), whereas in Europe it is a relatively common element among early Pleistocene faunal assemblages until 0.83 Ma (Turner and Antón 1996; Turner et al. 2008; Madurell-Malapeira et al. 2010).

Here we show that, for more than a century, the authorship of *P. brevirostris* has been incorrectly attributed to "Aymard, 1846" on the basis of a publication that never existed. In a strict sense, the original author and year of description of a taxon do not form part of its name. However, the International Code of Zoological Nomenclature (ICZN 1999) regulates their use (e.g., Article 51.3), further specifying that the citation of the authorship is optional, "although customary and often advisable" (Article 51.1). The Code therefore recommends reporting such data at least once in each work dealing with a taxon (Recommendation 51A), because this is important for distinguishing homonyms and identifying names that are not in their original combinations. Moreover, an accurate report of the year of publication of any taxon is also of utmost significance for applying the Principle of Priority (Article 23), which rules the use of synonyms and homonyms. Most journals dealing with systematic paleontology therefore strictly adhere to the recommendation to report original author and date, and in some cases—such as in the *Acta Palaeontologica Polonica* and the *Journal of Vertebrate Paleontology*—they further recommend or even require the corresponding citation to be included in the list of references. Accessing the original descriptions for taxa described in the 18th or 19th Century has been a problem for many scientists, especially those working in small institutions far from the large libraries of long established museums or universities. Such difficulties have, however, largely been ameliorated during the last decade, thanks to the free access provided by digital repositories to old literature that is nowadays in the public domain. The usefulness of such repositories—as well as the need to always check the original description—is illustrated here by the case of *P. brevirostris*.

Nomenclatural history

The purported original description.—The genus *Pachycrocuta* was erected by Kretzoi (1938: 118), who designated *Pachycrocuta brevirostris* as its type species ("genoholotypus"). Kretzoi (1938) attributed the authorship of the species to Aymard (without specifying the year of description or providing the citation in the list of references), as previously done by other authors (e.g., Gervais 1848–1852; Pictet 1853; Pomel 1853; Gaudry 1862; Weithofer 1889; Boule 1893; Soergel 1936). Subsequent authors similarly attributed the authorship of this binomen to Aymard, either without noting the year of publication (Brongersma 1937; Ficcarelli and Torre 1970; Pons-Moyà 1982; Turner and Antón 1996; Kretzoi and Kretzoi 2000; Palmqvist et al. 2011) or, more commonly, attributing it to 1846 (Kurtén

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1956, 1972; Howell and Petter 1980; Julià and Villalta 1984; Kurtén and Garevski 1989; Werdelin and Solounias 1991; Werdelin 1999; Stefen and Rensberger 1999; Turner 2001; Moullé et al. 2006; Arribas and Garrido 2008; Turner et al. 2008; Madurell-Malapeira et al. 2009; Werdelin and Peigné 2010)—just to report a selection of the most representative citations. Some of the above-mentioned authors (Howell and Petter 1980; Julià and Villalta 1984; Werdelin and Solounias 1991; Werdelin 1999; Arribas and Garrido 2008; Turner et al. 2008; Madurell-Malapeira et al. 2009) further reported the complete bibliographic reference that ought presumably to correspond to the original description of *Hyaena brevirostris*.

According to Howell and Petter (1980), *Hyaena brevirostris* was described by Aymard in a paper entitled "Communication sur le gisement de Sainzelles" [Communication on the site of Sainzelles], on pages 153–155 of volume 13 of *Annales de la Société d'Agriculture, Sciences, Arts et Commerce du Puy* in 1846. The remaining above-mentioned authors provided the same reference, or a similar one, with some variants regarding the name of the journal (Werdelin 1999; Arribas and Garrido 2008) and/or volume number (12 instead of 13; Turner et al. 2008; Madurell-Malapeira et al. 2009). When we tried to check this citation, we discovered that it did not exist in either volume 12 (supposedly published in 1846, but see below) or in volume 13 (apparently published in 1849)—or in any previous volume of that journal.

Aymard published a paper on an extinct artiodactyl (*Entelodon magnus*) in volume 12 of the above-mentioned journal, corresponding to the years 1842–1846, and dated to the year 1846. However, throughout the text there are several references to the year 1847, and as noted in Sherborn's (1924: 2160, 3825) *Index Animalium*—see also the searchable online version of Sherbon's compendium (http://www.sil.si.edu/digitalcollections/indexanimalium/), made available by the Smithsonian Institution Libraries—the accompanying wrapper indicates that it was not published until 1848. Besides *E. magnus* Aymard, 1848, this author further described other taxa (mainly in footnotes), such as the genus *Bothriodon* Aymard, 1848. In one of the footnotes, Aymard (1848: 259) referred to a previous report by him to the society on the fauna from Sainzelle—the type locality of *P. brevirostris*, spelled "Sainzelles" from Boule (1893) onwards—but did not describe or employ the nomen *Hyaena brevirostris*. In volume 13, Aymard did not report on the fauna from this site or name the species. Merely, in the proceedings of the *Société d'Agriculture, Sciences, Arts et Commerce du Puy* for the years 1847–1848, published in that volume, de Brive (1849) referred to a "notice" by Aymard on the circumstances that may have caused the accumulation of fossil bones at Sainzelles, although the binomen *Hyaena brevirostris* was not employed.

To our knowledge, the earliest paper by Aymard in which the name of the taxon was used is Aymard (1854a), published in volume 18 of the same journal—corresponding to the proceedings of year 1853, but with the cover date 1854. The title of this contribution, however, does not match that referred to the year 1846 by recent authors: "Acquisitions d'ossements fossiles trouvés à Sainzelle, commune de Polignac; aperçu descriptif sur ce curieux gisement et détermination des espècies fossiles qu'il renferme" [Acquisitions of fossil bones found at Sainzelle, town of Polignac; descriptive overview of this curious site and determination of the fossil species that it contains]. Galobart et al. (2003) are the only authors we found to refer the description of the species to 1853, whereas Savage and Russell (1983: 348, 356, 376) referred the authorship to "Aymard, 1854?"—the question mark presumably indicating uncertainties in the year of the description. Although neither of these authors provided the bibliographic reference, they were most likely referring to Aymard (1854a), because Aymard (1854b) did not mention this taxon. However, Aymard (1854a) did not provide any description or indication for the name of the taxon, so that *Hyaena brevirostris* Aymard, 1854a does not fulfill the criteria of nomenclatural availability for names published before 1931 (ICZN, 1999: article 12)—which require the publication of the name "accompanied by a description or a definition … or by an indication" (Article 12.1).

Finally, according to Gaudry (1862) and Weithofer (1889), the binomen *Hyaena brevirostris* was erected somewhat later by Aymard, in the 22nd session of the *Congrès scientifique de France* of year 1855, published the following year (Anonymous 1856: 271). Aymard certainly mentioned the name of the species in the proceedings of that meeting (Anonymous 1856: 271, our translation from the French original): "a species, erected on the basis of an almost complete cranium (*hyaena* [sic!] *brevirostris*. Aym.) has been confirmed by the concordant observations by Mr. Gervais and Mr. Pictet". According to the Code, if a name is made available in a report of a meeting, the person responsible for the name (and not the secretary or reporter) is the author of the name (Article 50.2). However, like his previous publication (Aymard 1854a), such a short note does not fulfill the criteria of availability, so that *Hyaena brevirostris* Aymard, 1856 must also be considered a nomen nudum.

The true original description.—The erroneous attribution of the taxon's authorship to "Aymard, 1846" by most recent authors probably stems from an incorrect interpretation of Boule's (1893) introductory lines in the first detailed description of the holotype cranium of *Hyaena brevirostris*. According to Boule (1893: 85, our translation from the French original), Aymard discovered the cranium ca. 1845 in the surroundings of Le Puy, being "deposited in the Musée du Puy and registered with the name *Hyaena brevirostris*, Aym." Boule (1893) noted that Aymard reported on this cranium in several notes, but the only bibliographic citation provided by him was volume 12 (attributed by him to year 1846) of the above-mentioned annals—which, as already explained, were published in 1848 and do not include any mention of this taxon. Boule's (1893) citation of Aymard was reproduced (also without title) by Kurtén (1972: 120) as the original description of this species, although the latter author was cautious enough as to state that he had not actually seen it ("not seen; fide Boule, 1893"). At some point, however, an erroneous title became associated with the author Aymard and the year 1846, which was subsequently copied from one author to another. To our knowledge, Howell and Petter (1980) were the first authors to publish the incorrect reference for the original description of the species. These authors might have mixed the year provided by Kurtén (1972) while referring in fact to the contribution by Aymard (1854a). The latter begins without a title—which is however stated in the summary provided two pages before in the same journal—and this might explain why either Howell and Petter (1980), or some other previous authors, eventually provided a different generic title for Aymard's contribution. In any case, the significance of Boule's (1893: 86) comment on the fact that paleontologist Paul Gervais had studied the cranium and "was able to give a short diagnosis in the first edition of his Paléontologie française" remained unnoticed by most researchers, probably because of the fact that Gervais (1848–1849), Pictet (1853), and Boule (1893) all attributed the taxon to Aymard.

The attribution of the authorship to Aymard notwithstanding, when referring to the taxon Pictet (1853: 223) only provided a reference to Gervais' book. Although succinct, the description provided by the latter (Gervais 1848–1852: 122, our translation from the French original) is enough to confer availability to the name *Hyaena brevirostris*: "Fossil from Sainzelle, town of Polignac, near of Le Puy. I have studied in the museum of this town two hyena cranial fragments from Sainzelle: they indicate a size at least equal to that of *H. spelaea*; but the upper jaw has a transverse molar very similar to that of *H. fusca* and *vulgaris*. The lower carnassial is 0.030 m long, and the upper one 0.045 m long; the vertical plane of the lower jaw is very elevated." The fact that Gervais (1848–1852) attributed the authorship to Aymard is irrelevant for nomenclatural purposes, since the author of a name is the person who first published it in a way that satisfies the criteria of availability (Article 50.1). Only "if it is clear from the contents that some person other than an author of the work is alone responsible for both the name [...] and for satisfying the criteria of availability other than actual publication, then that other person is the author of the name or act. If the identity of that other person is not explicit in the work itself, then the author is deemed to be the person who published the work." (Article 50.1.1). Gervais (1848–1852: 122) first employed the name without referring it to any author, and only in the following line he stated "*H. brev.*, Aymard, *Mus. du Puy.*"—i.e., he referred to a museum label or record, instead of providing the bibliographic citation, as he customarily did for other taxa. This fact indicates that Gervais was providing a description based on his own observations—instead of referring to any previous publication by Aymard—and that he merely referred the authorship to the latter on the basis of a museum label or record. The reference to a geological horizon, or specimen label cannot be considered an indication in the sense of the Code (Article 12.3), and given that there is no explicit statement in Gervais (1848–1852) attributing the description to Aymard, in application of the above-mentioned Article 50.1.1, the authorship of *Hyaena brevirostris* must be attributed to Gervais.

Gervais' (1848–1852) book was issued in several parts during successive years. In those cases, the Code dictates that the date of publication of each part is to be separately determined (Article 21.5). According to Wagner (1851), the part dealing with carnivorans was published in 1850, and hence the nomen *Hyaena brevirostris* must be attributed to "Gervais, 1850." This is further confirmed by Sherborn's (1924: 885) *Index Animalium*, in which this author (and not Aymard) is credited for the authorship of the taxon. To our knowledge, Sherborn's (1924) brief statement is the only previous instance in which the authorship of *Hyaena brevirostris* has been correctly attributed to Gervais instead of Aymard.

Conclusions

Although it is not mandatory, the International Code of Zoological Nomenclature (ICZN, 1999) recommends providing the author and year of original description of any taxon, when first mentioned in a publication. This is useful for several reasons, both taxonomic (i.e., information retrieval) and nomenclatural (e.g., determination of priority of synonyms and homonyms). Here we show that the authorship of the extinct hyaenid *Pachycrocuta brevirostris* has been incorrectly attributed to "Aymard, 1846" for more than a century, on the basis of a publication that never existed. Our bibliographic research indicates that the first publication in which the name is employed—*Zoologie et Paléontologie françaises* by Gervais (1848–1852; the part dealing with carnivorans being published in 1850)—fulfils the criteria of availability. Subsequent use of the same binomen by Aymard (1854a) does not fulfill the criteria of availability and, in any case, it would not have priority over Gervais (1848–1852). Given that the latter author did not attribute the description to Aymard, but merely employed the latter's name in reference to a museum label/record (which does not constitute a valid indication), the correct name with authorship for this taxon must be *Pachycrocuta brevirostris* (Gervais, 1850).

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References

Anonymous 1856. La paléontologie de la Haute-Loire offre-t-elle, pour certains époques, des caractères qui la particularisent? *In*: *Congrès Scientifique de France. Vingt-deuxième Session, Tenue au Puy en Septembre 1955. Tome Premier*, 261–277. Derache, Paris.

Arribas, A. and Garrido, G. 2008. Hiénidos [*Pachycrocuta brevirostris* (Aymard, 1846) y *Hyaena brunnea* Thunberg, 1820] del yacimiento de Fonelas P-1 (Cuenca de Guadix, Granada). *In*: A. Arribas (ed.), Vertebrados del Plioceno Superior Terminal en el Suroeste de Europa: Fonelas P-1 y el Proyecto Fonelas. Instituto Geológico y Minero de España, Madrid. *Cuadernos del Museo Geominero* 10: 201–230.

Aymard, A. 1848. Essai monographique sur un nouveau genre de Mammifère fossile trouvé dans la Haute-Loire, et nommé *Entélodon*. *Annales de la Société d'Agriculture Sciences, Arts et Commerce du Puy* 12: 227–268.

Aymard, M. 1854a. Acquisitions d'ossements fossiles trouvés à Sainzelle, commune de Polignac; aperçu descriptif sur ce curieux gisement et détermination des espècies fossiles qu'il renferme. *Annales de la Société d'Agriculture Sciences, Arts et Commerce du Puy* 18: 51–54.

Aymard, A. 1854b. Des terrains fossilifères du bassin supérieur de la Loire. *Comptes Rendus des Séances de l'Académie des Sciences Paris* 38: 673–677.

Boule, M. 1893. Description de l'*Hyaena brevirostris* du Pliocène de Sainzelles près le Puy (Haute-Loire). *Annales des Sciences Naturelles Zoologie et Paléontologie* 15: 85–97.

Brongersma, L.D. 1937. On fossil remains of a hyaenid from Java. *Zoologische Mededelingen* 20: 186–202.

Brive, A. de 1849. Compte-rendu des travaux de la Société lu le même jour. *Annales de la Société d'Agriculture Sciences, Arts et Commerce du Puy* 13: 9–36.

Ficcarelli, G. and Torre, D. 1970. Remarks on the taxonomy of hyaenids. *Palaeontographia Italica* 66: 13–33.

Galobart, À., Antón, M., and Maroto, J. 2003. Hiénidos y cánidos de los yacimientos de Incarcal (Girona, NE de la Península Ibérica). Una aproximación a la paleobiología del hiénido del Pleistoceno inferior. *Paleontologia i Evolució* 34: 79–98.

Gaudry, A. 1862. *Animaux Fossiles et Géologie de l'Attique, d'après les Recherches Faites en 1855–56 et 1860*. 474 pp. F. Savy, Paris.

Gervais, P. 1848–1852. *Zoologie et Paléontologie Françaises. Nouvelles Recherches sur les Animaux Vivants et Fossiles de la France. Tome I. Contenant l'Énumerération Méthodique et Descriptive des Espèces ainsi que les Principes de leur Distribution Géographique et Paléontologique*. 271 pp. Arthus Bertrand, Paris.

Howell, F.C. and Petter, G. 1980. The *Pachycrocuta* and *Hyaena* lineages (Plio-Pleistocene and extant species of the Hyaenidae). Their relationships with Miocene ictitheres: *Palhyaena* and *Hyaenictitherium*. *Geobios* 13: 579–623.

International Commission on Zoological Nomenclature (ICZN) 1999. *International Code of Zoological Nomenclature. Fourth Edition*. 306 pp. The International Trust for Zoological Nomenclature, London.

Julià, R. and Villalta, J.F. de 1984. El yacimiento de vertebrados del Pleistoceno inferior de Crespià (Girona, NE de la Península Ibérica). *Acta Geològica Hispànica* 19: 129–138.

Kretzoi, M. 1938. Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtfauna. *Annales Musei Nationalis Hungarici* 31: 88–157.

Kretzoi, M. and Kretzoi, M. 2000. *Index Generum et Subgenerum Mammalium; Pars 137, Section 1*. 433 pp. Backhuys Publishers, Leiden.

Kurtén, B. 1956. The status and affinities of *Hyaena sinensis* Owen and *Hyaena ultima* Matsumoto. *American Museum Novitates* 1764: 1–48.

Kurtén, B. 1972. Fossil Hyaenidae from the excavations at Stránská Skála. *Anthropos* 20: 113–120.

Kurtén, B. and Garevski, R. 1989. Giant hyena, *Hyaena brevirostris* Aymard (Mammalia, Carnivora), from the Middle Pleistocene of Manastirec, Yugoslavia. *Annales Zoologici Fennici* 26: 145–147.

Madurell-Malapeira, J., Alba, D.M., and Moyà-Solà, S. 2009. Carnivora from the late Early Pleistocene of Cal Guardiola (Terrassa, Vallès-Penedès Basin, Catalonia, Spain). *Journal of Paleontology* 83: 969–974.

Madurell-Malapeira, J., Minwer-Barakat, R., Alba, D.M., Garcés, M., Gómez, M., Aurell-Garrido, J., Ros-Montoya, S., Moyà-Solà, S., and Berástegui, X. 2010. The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe. *Quaternary Science Reviews* 29: 2972–2982.

Moullé, P.-E., Lacombat, F., and Echassoux, A. 2006. Apport des grands mammifères de la grotte du Vallonnet (Roquebrune-Cap-Martin, Alpes-Maritimes, France) à la connaissance du cadre biochronologique de la seconde moitié du Pléistocène inférieur d'Europe. *L'Anthropologie* 110: 837–849.

Napoleone, G., Albianelli, A., Azzaroli, A., Bertini, A., Magi, M., and Mazzini, M. 2003. Calibration of the Upper Valdarno basin to the Plio-Pleistocene for correlating the Apennine continental sequences. *Il Quaternario* 16: 131–166.

Palmqvist, P., Martínez-Navarro, B., Pérez-Claros, J.A., Torregrosa, V., Figueirido, B., Jiménez-Arenas, J.M., Espigares, M.P., Ros-Montoya, S., and De Renzi, M. 2011. The giant hyena *Pachycrocuta brevirostris*: Modelling the bone-cracking behavior of an extinct carnivore. *Quaternary International* 243: 61–79.

Pictet, F.-J. 1853. *Traité de Paléontologie ou Histoire Naturelle des Animaux Fossiles Considerés dans leurs Rapports Zoologiques et Géologiques. Tome Premier. Seconde Édition.* 584 pp. J.-B. Baillière, Paris.

Pomel, A. 1853. *Catalogue Méthodique et Descriptif des Vertébrés Fossiles Découverts dans le Bassin Hydrographique Supérieur de la Loire, et surtout dans la Vallée de son Affluent Principal, l'Allier.* 193 pp. J.-B. Baillière, Paris.

Pons-Moyà, J. 1982. Hyaenidae (Carnivora, Mammalia) del Pleistoceno Inferior de Cueva Victoria (Murcia, España). *Endins* 9: 45–48.

Savage, D.E. and Russell, D.E. 1983. *Mammalian Paleofaunas of the World*. 432 pp. Addison-Wesley Publishing Company, Reading.

Sherborn, C.D. 1924. Section 2, Pt. 4 (1801–1850), Index Bail.-Byzos. *In*: *Index Animalium*, 641–943. Trustees of the British Museum, London.

Soergel, W. 1936. *Hyaena brevirostris* Aymard und *Hyaena* ex aff. *Crocotta* Erxl. aus den Kiesen von Süßenborn. *Zeitschrift der Deutschen Geologischen Gesellschaft* 88: 525–539.

Stefen, C. and Rensberger, J.M. 1999. The specialized structure of hyaenid enamel: description and development within the lineage–including percrocutids. *Scanning Microscopy* 13: 363–380.

Turner, A. 2001. Remains of *Pachycrocuta brevirostris* (Mammalia, Hyaenidae) from the Lower Pleistocene site of Untermassfeld near Meiningen. *In*: H.D. Kahlke and R.D. Kahlke (eds.), *Das Pleistozän von Untermassfeld in Thuringen*, 673–690. Rudolf Harbelt Verlag, Bonn.

Turner, A. and Antón, M. 1996. The giant hyaena, *Pachycrocuta brevirostris* (Mammalia, Carnivora, Hyaenidae). *Geobios* 29: 455–468.

Turner, A., Antón, M., and Werdelin, L. 2008. Taxonomy and evolutionary patterns in the fossil Hyaenidae of Europe. *Geobios* 41: 677–687.

Wagner, A. 1851. Bericht über die Leistungen in der Naturgeschichte der Säugthiere während des Jahres 1850. *Archiv für Naturgeschichte* 17 (1): 1–32.

Weithofer, K.A. 1889. Die fossilen Hyänen des Arnothales in Toskana. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe* 55: 337–357.

Werdelin, L. 1999. *Pachycrocuta* (hyaenids) from the Pliocene of east Africa. *Paläontologische Zeitschrift* 73: 157–165.

Werdelin, L. and Lewis, M. 2005. Plio-Pleistocene Carnivora of eastern Africa: species richness and turnover patterns. *Zoological Journal of the Linnean Society* 144: 121–144.

Werdelin, L. and Peigné, S. 2010. Carnivora. *In*: L. Werdelin and W.J. Sanders (eds.), *Cenozoic Mammals of Africa*, 603–657. University of California Press, Berkeley.

Werdelin, L. and Solounias, N. 1991. The Hyaenidae: taxonomy, systematics and evolution. *Fossils and Strata* 30: 1–104.

David M. Alba [david.alba@icp.cat], Institut Català de Paleontologia Miquel Crusafont, ICTA-ICP, c/ Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain; Dipartimento di Scienze della Terra, Università di Torino, Via Valperga Caluso 35, 10125 Torino, Italy.

Víctor Vinuesa [victor.vinuesa@icp.cat] and Joan Madurell-Malapeira [joan.madurell@icp.cat], Institut Català de Paleontologia Miquel Crusafont, ICTA-ICP, c/ Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain.

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Chapter 9. The endocranial morphology of the Plio-Pleistocene bone-cracking hyena *Pliocrocuta perrieri*: Behavioral implications

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Summary: This work investigates the inner cavities of the skull of *Pliocrocuta perrieri*, with emphasis on the description and comparison of the brain and frontal sinus morphology of this taxon with those of extant hyaenids.

Author's contribution: The doctoral candidate is the first author of this work, and was directly involved in all the stages of its development, including the design of the paper, the CT processing and 3D modelling, the morphometric comparisons, and the writing of the manuscript.

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ORIGINAL PAPER

The Endocranial Morphology of the Plio-Pleistocene Bone-Cracking Hyena *Pliocrocuta perrieri*: Behavioral Implications

**Víctor Vinuesa · Joan Madurell-Malapeira ·
Josep Fortuny · David M. Alba**

Abstract The internal cranial morphology of the bone-cracking hyena *Pliocrocuta perrieri* (Carnivora, Hyaenidae) is described based on three crania from the late Pliocene and early Pleistocene of the Iberian Peninsula. The shape and size of the inner cranial cavities (with emphasis on encephalization and relative regional brain volumes) are compared with those of extant hyaenids with the aid of computed tomography techniques—which had not been previously used to study the brain morphology of any extinct bone-cracking hyena. Our results indicate that the frontal sinuses of *P. perrieri* are caudally extended and overlap the brain cavity, as in other extinct and extant bone-cracking hyaenids. In turn, the brain morphology and sulcal pattern of *P. perrieri* are more similar to those of *Hyaena hyaena* and *Parahyaena brunnea* than to those of *Crocuta crocuta* among extant bone-cracking hyaenids. Our results further indicate that *Pliocrocuta* is clearly less encephalized than the highly-social *Crocuta*, and displays an anterior cerebrum relatively smaller than in all extant bone-cracking hyenas (indicating the possession of a poorly-developed frontal cortex). These facts might suggest that *P. perrieri* possessed less developed cognitive abilities than *Crocuta* for processing the information associated with complex social behaviors.

Keywords Carnivora · Hyaenidae · CT-scan · Brain · Frontal sinus

V. Vinuesa · J. Madurell-Malapeira · J. Fortuny · D. M. Alba
Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/ de les columnes s/n, Campus de la UAB, 08193, Cerdanyola del Vallès Barcelona, Spain

J. Madurell-Malapeira (✉)
Dipartimento di Scienze della Terra, Sapienza Università di Roma, Piazzale Aldo Moro 5, 00185 Roma, Italy
e-mail: joan.madurell@icp.cat

Introduction

Hyaenid biodiversity (with over 60 extinct species documented) has decreased from the Miocene to the Holocene, with a concomitant reduction in their ecomorphotype diversity (from six to merely two extant) (Werdelin and Solounias 1996). Hunting (or cursorial) hyenas were the last ecomorphotype to become extinct, being substituted by canids during the Pliocene, after the dispersal of the latter into the Old World by the end of the Miocene (Werdelin and Turner 1996a, b; Turner et al. 2008). Three out of the four extant hyaenids belong to the bone-cracking ecomorphotype: *Crocuta crocuta* (Erxleben, 1777)*, Hyaena hyaena* (Linnaeus, 1758), and *Parahyaena brunnea* (Thunberg, 1820). Many extinct hyaenids have also been inferred to belong to this ecomorphotype, including *Adcrocuta eximia* (Roth and Wagner, 1854)*, Allohyaena kadici* Kretzoi, 1938, *Pliocrocuta perrieri* (Croizet and Jobert, 1828), and *Pachycrocuta brevirostris* (Gervais, 1850). Due to their overall morphological similarity, resolving the phylogenetic relationships between these fossil taxa and their extant relatives has proven controversial (see Turner et al. 2008 for the most recent phylogenetic analysis of extinct European hyaenids).

Internal cranial morphology might potentially contribute additional data for further clarifying the phylogenetic relationships among extant and extinct hyaenids, which are customarily inferred on the basis of external craniodental anatomy. However, the morphology and size of internal cranial cavities in this group has not been extensively investigated (at least with regard to brain morphology), because frontal sinuses have been the focus of most previous research (Joeckel 1998; Antón et al. 2006; Dockner 2006). Paulli 1900 first described the presence of extensive and elongated cranial sinuses in hyaenids, and this feature was subsequently documented in many extant and extinct taxa (Werdelin 1989;

Werdelin and Solounias 1991; Joeckel 1998; Antón et al. 2006; Dockner 2006). With regard to brain morphology in extinct hyaenids, before computer-tomography (CT) techniques became widespread in paleontological research, such studies were based on brain endocasts. Most research on this subject was carried out by Radinsky, who nevertheless focused on carnivorans in general (Radinsky 1971, 1977) and felids in particular (Radinsky 1975), but not specifically on hyaenids. More recently, studies on the internal cranial anatomy of hyaenids relied on extant taxa (Holekamp et al. 2007a; Arsznov et al. 2010; Sakai et al. 2011), so that the brain morphology of extinct bone-cracking hyenas remains undescribed.

Here, with the aid of CT-scans, we describe the internal cranial morphology (frontal sinuses and brain) of the extinct bone-cracking hyena *Pliocrocuta perrieri*, which is the most common hyena in late Pliocene to early Pleistocene mammalian faunas from Europe (Turner et al. 2008). We analyze three complete crania of this hyaenid species from the Iberian Peninsula, whose external morphology was previously described by Vinuesa et al. (2014). The frontal sinus and brain morphology of these specimens is compared with that of extant hyaenids. Their internal cranial morphology (and, in particular, regional brain proportions and sulcal pattern) can be employed to make paleobiological inferences on the behavior of these taxa, as previously shown for extant hyaenids (Sakai et al. 2011). Moreover, their phylogenetic implications are also discussed.

Materials and Methods

Studied Sample

The described endocasts were derived from three crania housed at the Institut Català de Paleontologia Miquel Crusafont in Sabadell (Spain). IPS36758 and IPS36759 come from the classic Iberian locality of Villarroya (late Pliocene, MN16; Arribas Herrera and Bernad García 1994; Jiménez García et al. 1999; Agustí and Oms 2001; Anadón et al. 2009), whereas IPS27340 was found in La Puebla de Valverde (early Pleistocene, MN17; Crusafont Pairó et al. 1964; Gautier and Heintz 1974; Sinusía et al. 2004). The comparative sample includes CT-scans of extant bone-cracking hyenas, kindly provided by the Digimorph Team (www.digimorph.org): *Crocuta crocuta* (MVZ 184551, University of California Berkeley, Museum of Vertebrate Zoology, Berkeley, USA), *Parahyaena brunnea* (MVZ 117842, University of California Berkeley, Museum of Vertebrate Zoology, Berkeley, USA), and *Hyaena hyaena* (USNM 182034, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA).

CT-Scanning and Reconstruction of Internal Cranial Features

IPS36759 was CT-scanned at the Mútua de Terrassa hospital (Terrassa, Spain), using a Siemens Sensation 16 at 140 kV and 300 mA. A total of 999 slices of 0.3 mm in width, with an interslice space of 0.3 mm, were obtained, resulting in an output image of 512×512 pixels per slice and a pixel size of 0.43 mm. The other crania were CT-scanned at the ICP (Sabadell), using an industrial CT scanner YXLON Y.TU 450-D09, at 350 kV and 2 mA (IPS36758) and 430 kV and 3 mA (IPS27340). A total of 1,128 slices with an interslice space of 0.25 mm, 720 projections, and 50 msec of integration time were obtained for IPS36758, resulting in an output image of 1,536×1,536 pixels per slice and a pixel size of 0.27 mm. For IPS27340, a total of 1,020 slices, with an interslice of 0.3 mm, 720 projections, and 50 msec of integration time were obtained, resulting in an output image of 1,536×1,536 pixels per slice and a pixel size of 0.26 mm.

The extant taxa were scanned at the The University of Texas High-Resolution X-ray Computed Tomography Facility - Digital Morphology Group using the ACTIS CT scanner. For detailed scan parameters and further information, visit www.digimorph.org.

3D virtual models of the cranium and the endocranial cavities were derived from the CT-scans, using Hounsfield units as reference units. Image processing and 3D modeling were performed using semiautomatic tools provided by Avizo 7.0 (VSG, France) to segment the differences between bone and infilled matrix. Avizo 7.0 (VSG, France) was also used to generate 3D surfaces and volumes using the same steps for each CT-scan. External brain morphology was inferred from both virtual endocasts and CT-slices, and total and regional brain volumes were computed for all specimens. Due to poor and incomplete preservation in one side of both IPS36758 and IPS27340, the virtual endocasts of these specimens were sagittally cut to compute the brain cavity volume of the well preserved side, which was then doubled to estimate the complete volume of the whole brain. In these specimens, mirroring was also used for visualization purposes. Rhinoceros 5.0 (McNeel, USA) was used to perform orientation, mirroring, and volume measurements of all the analyzed specimens. Although 3D models of the frontal sinuses were also derived, due to the lack of sufficient resolution, their inner subdivisions were evaluated solely on the basis of CT-images.

Statistical Analyses

Encephalization

When comparing brain size between taxa of different size, in order to make paleobiological inferences on cognitive abilities and/or behavior, it is necessary to take size-scaling considerations into account (Jerison 1973; Gould 1975; Alba 2010).

Therefore, to compare the total endocranial volume of *Pliocrocuta* with those of extant bone-cracking hyenas, we relied on allometric techniques (Gould 1966; Klingenberg 1998). Accordingly, bivariate allometric plots of mean species total brain cavity volume vs. body mass were derived, after logarithmically transforming these variables (using decimal logarithms, log). For *Pliocrocuta*, brain cavity volume was computed from the virtual endocasts derived in this paper. Body mass for this taxon was estimated based on bivariate regressions of mean-species body mass (data taken from Van Valkenburgh 1990) vs. basal skull length (data taken from Sakai et al. 2011) in extant bone-cracking hyenas. *Proteles* Geoffroy Saint-Hilaire, 1824, was excluded from the regression derived in this paper because it displays divergent cranial proportions that resulted in prediction errors that were too high for extant hyaenids.

Allometric regression equations of encephalization were computed separately for extant felids and for other (non-felid, non-hyaenid) extant feliform carnivorans (Eupleridae, Herpestidae, Viverridae and Prionodontidae) together, because the former display a clear allometric grade shift of encephalization as compared to the latter—i.e., similar allometric relationships (slope) but with a clearly higher elevation (intercept). This allometric grade shift was statistically tested by means of analysis of covariance (ANCOVA). No regression equation was computed for hyaenids, because of the small number of extant taxa and also because *Proteles* clearly shows a lesser degree of encephalization than bone-cracking hyaenids. Therefore, we relied on allometric residuals to compare the encephalization of both extant and extinct hyaenids with those of other feliforms. Allometric residuals of total endocranial volume vs. body mass, based on the non-felid feliform regression as the baseline, were employed as metrics of encephalization for these taxa as well as for both extant and extinct hyaenids. Data for extant non-hyaenid feliform carnivorans (including felids) were taken from Finarelli and Flynn (2009), whereas data for hyaenids were taken from Sakai et al. (2011). Residuals for all feliform carnivorans were analyzed by means of boxplots as well as analysis of variance (ANOVA). All statistical computations were made with the SPSS v. 16.0 statistical package.

Residuals of encephalization are the log-transformed equivalent of Jerison's (Jerison 1973) encephalization quotients (Finarelli and Flynn 2009), but the former are to be preferred becaue they reflect positive and negative deviations from the best-fit line symmetrically around zero. To compute best-fit lines, we employed linear regression (ordinary least squares) instead of reduced major axis (e.g., Martin and Barbour 1989), because the former technique is more suitable when making predictions of one variable from another (Warton et al. 2006), such as when estimating body mass or when computing residuals (in which best-fit lines, with body size as the independent variable, are used as a criterion of subtraction; Gould 1966; Smith 1984; Alba 2010).

Regional Brain Volumes

Virtual endocasts were subdivided into the following three regions, in agreement with previous literature (Arsznov et al. 2010; Sakai et al. 2011; Swanson et al. 2012), following sulcal patterns and/or bony landmarks: anterior cerebrum, posterior cerebrum, and cerebellum plus brain stem. To do so, endocasts were oriented so that the maximum length of the cerebrum plus the olfactory bulbs was situated along the horizontal plane. The anterior cerebrum was defined as the region situated caudally with respect to the olfactory bulbs and cranially with regard to the junction of the cruciate sulcus and the sagittal plane, whereas the posterior cerebrum region was defined as the region situated caudally from the cruciate sulcus and extending to the cerebellum (more precisely, the tentorium; Sakai et al. 2011). The cerebellum plus brain stem region includes the volume of these two regions, placed at the posterior cranial fossa, which goes from the most anterior border of the tentorium to the foramen magnum (Sakai et al. 2011). Finally, the volume of the cerebrum corresponds to the sum of the anterior and posterior cerebrum volumes. Total and regional brain volumes for extant hyenas were taken from Sakai et al. (2011). To compute regional brain volumes in the fossil specimens, we relied on a ratio of the volume of each region relative to total brain cavity volume (which includes the olfactory bulbs, the cerebrum, the cerebellum, and the brain stem), following Sakai et al. (2011).

Results

Description of the Internal Cranial Morphology

IPS36759 is generally well preserved, while IPS36758 and IPS27340 display significant distortion in some areas (Vinuesa et al. 2014). In spite of this fact, an accurate description of their internal morphology is possible by combining data from sagittal and coronal CT sections (Fig. 1) with virtual 3D reconstructions (Fig. 2) for the three specimens. We provide below a description of both the frontal sinuses and the brain (cerebrum, cerebellum, and medulla oblongata).

The overall shape of the frontal sinuses can be observed in the three studied skulls (Fig. 1a-g), although the preservation is poorer in IPS36758 and IPS27340 (due to bone fractures and missing portions). Accordingly, the description of the frontal sinuses below is mostly based on IPS36759, in which they are generally well preserved, except for their limit with the nasal fossa and the presence of a fracture (Figs. 1a, c). Overall, the frontal sinuses of *P. perrieri* are very extensive and completely overlay the brain cavity, by extending from the anterior portion of the frontals to the parietals and also reaching the nuchal crests (this can be seen also in IPS27340 and IPS36758; Fig. 1f, g). These sinuses are divided into two

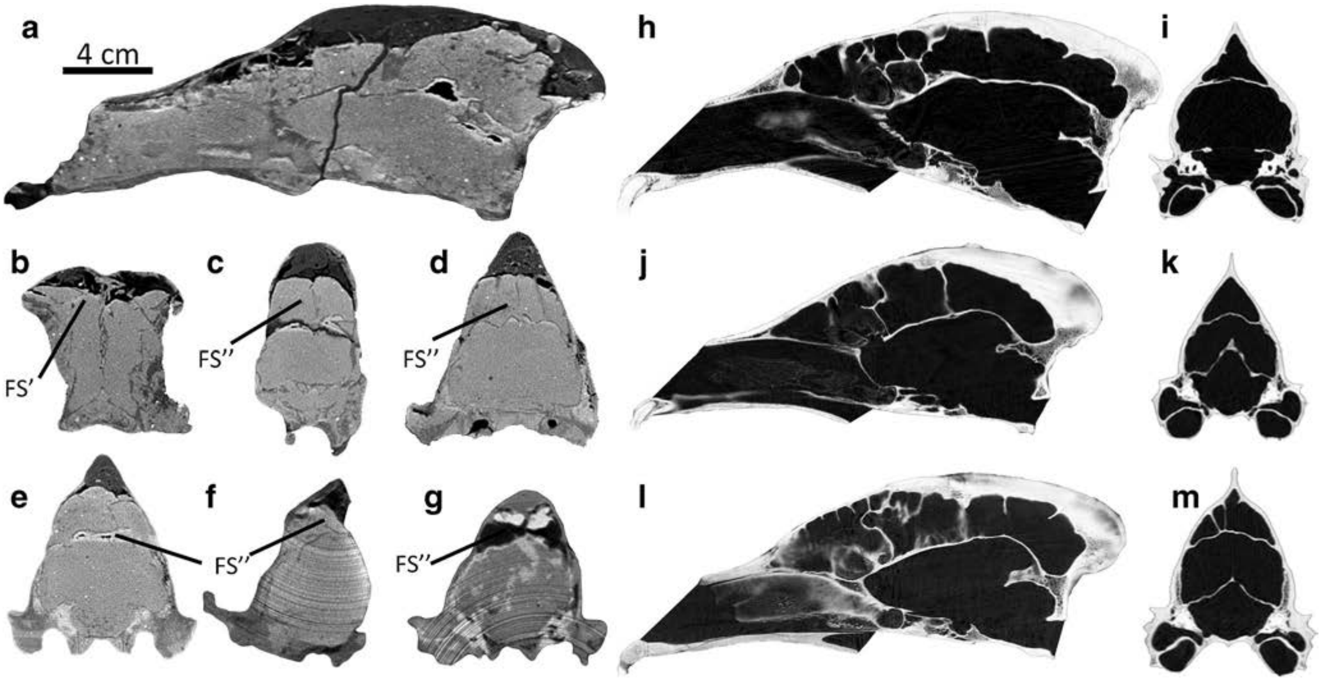

Fig. 1 CT-scan slices of the crania of *Pliocrocuta perrieri*, compared to those of extant bone-cracking hyaenids. (**a**–**d**), *Pliocrocuta perrieri*: (**a**), Sagittal slice of IPS36759; (**b**), Coronal slice of IPS36759 at the postorbital process of the frontal; (**c**), Coronal slice of IPS36759 at the postorbital constriction width; (**d**), Coronal slice of IPS36759 at the retroarticular process level. (**e**–**g**), Coronal slices at the tympanic bullae level in *P. perrieri*: (**e**), IPS36759; (**f**), IPS27340; (**g**), IPS36758. (**h**–**i**), *Crocuta crocuta*: (**h**), Sagittal slice; (**i**), Coronal slice at the tympanic bullae; (**j**–**k**), *Hyaena hyaena*: (**j**), Sagittal slice; (**k**), Coronal slice at the tympanic bullae; (**l**–**m**), *Parahyaena brunnea*: (**l**), Sagittal slice; (**m**), Coronal slice at the tympanic bullae. Abbreviations: *FS* rostral sinus region, *FS* nuchal sinus region

(anterior and posterior) regions, as in extant bone-cracking hyenas (Paulli 1900). The anterior region is strongly pneumatized, by displaying small and chaotic chambers (Fig. 1b). The posterior one is less pneumatized and displays larger and more structured chambers (Fig. 1c-e), which are symmetrical and located over the whole length of the brain. The coronal sections of the posterior region show that there are two symmetrical anterior chambers (Fig. 1c), which extend until the level of maximum brain width. More posteriorly (Fig. 1d), they are replaced by four (two central and two lateral) additional chambers, with their walls being obliquely oriented with regard to the sagittal plane. Posteriorly, these lateral chambers become progressively smaller, whereas the central ones become larger until occupying the entire cavity (Fig. 1e).

The preservation of the brain cavity in the three studied specimens is generally good, so that all the main brain subdivisions (the olfactory bulbs, the cerebrum, the cerebellum, and the medulla oblongata) can be readily distinguished in spite of some preservation issues. IPS36758 (Fig. 2b–d) is slightly compressed dorsoventrally and lacks a significant portion of the left anterior region, which is also somewhat distorted (Fig. 2c). In contrast, the right side of this specimen is relatively well preserved (Fig. 2b), allowing us to discern some of the major sulci, although incompletely, with the inferior portion of the presylvian-sylvian sulci lacking. The brain cavity of IPS36759 (Fig. 2e-g) is the best preserved, so that despite slight distortion and the presence of various small fractures at the top of the cranial vault, almost all the complete brain morphology can be adequately observed in at least one side. IPS27340 (Fig. 2h–j), like IPS36758, lacks a significant portion of the endocast (from the right side; Fig. 2h), because the braincase is partially broken away. The left side of this specimen, however, is completely preserved (enabling us to compute its volume) and further allows us to recognize several morphological features, such as the cruciate and the suprasylvian sulci (Fig. 2i).

In spite of some preservational problems mentioned above, the whole endcoranial morphology of *P. perrieri* can be confidently described by combining the data provided by the three available specimens (Fig. 2k, l), which enable the distinction of the sylvian, ectosylvian, suprasylvian, coronal, ectolateral, ansate, cruciate and presylvian sulci, as well as of a large portion of the longitudinal fissure. The morphological description provided below is mostly based on the best preserved specimen (IPS36759), but further includes remarks based on the other two specimens when possible.

In both IPS36759 and IPS27340, the presylvian sulcus forms a dorsally-concave curve that runs from the dorsal portion of the anterior cerebrum towards the frontobasal portion of the posterior cerebrum, below the coronal and suprasylvian sulci (Fig. 3b, c). In the three specimens (only partially in

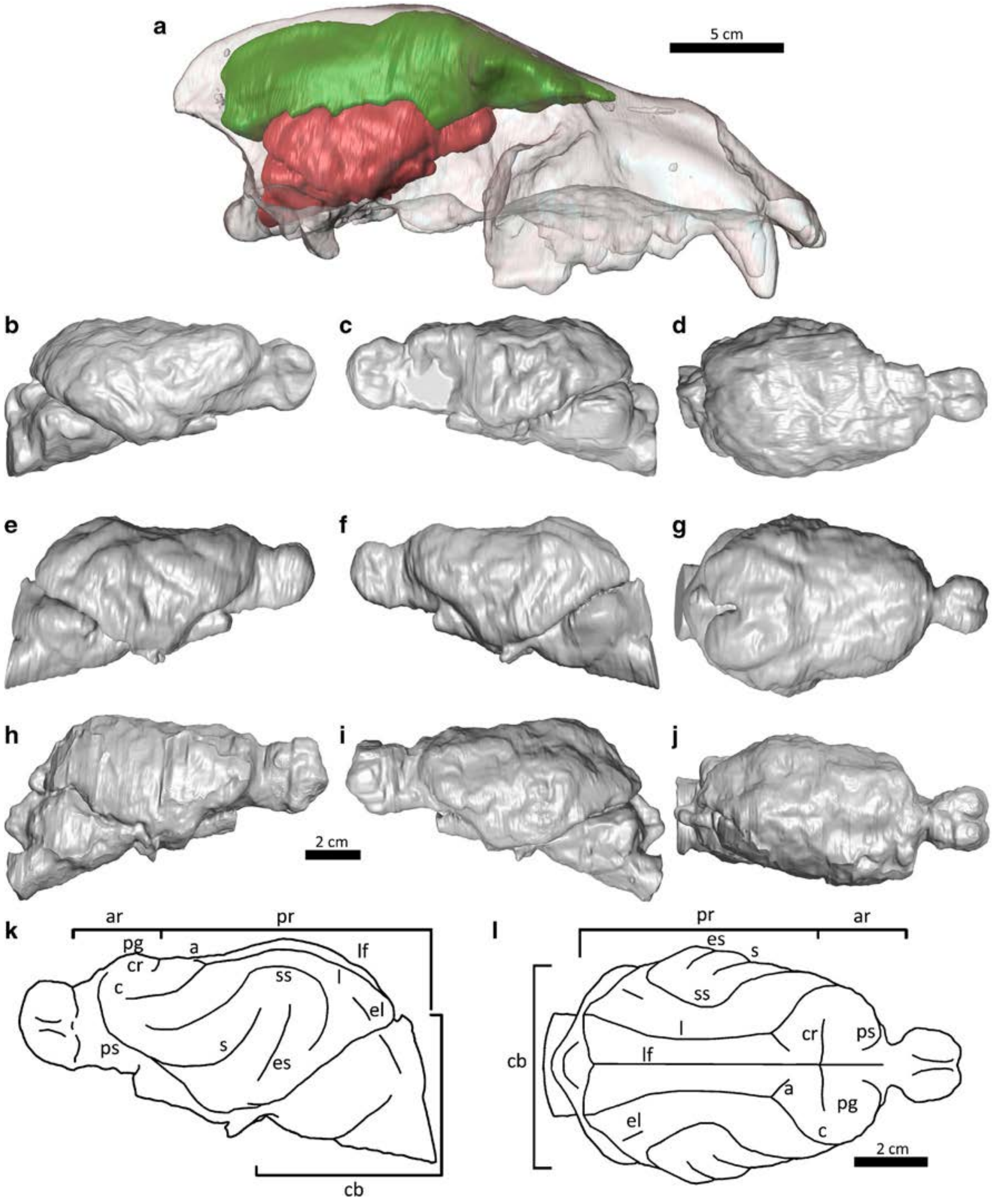

Fig. 2 Internal cranial morphology of *Pliocrocuta perrieri*. (**a**), Cranium of IPS36759 in right lateral view (translucent), showing the brain cavity (red) and the frontal sinuses (green); (**b–d**), Virtual endocast of IPS36758 in (**b**), right lateral; (**c**), left lateral; (**d**), dorsal views; (**e–g**), Virtual endocast of IPS36759 in (**e**), right lateral; (**f**), left lateral; (**g**), dorsal views; (**h–j**), Virtual endocast of IPS27340 in (**h**), right lateral; (**i**), left lateral; (**j**), dorsal views; (**k–l**), Schematic depiction of the brain sulcal pattern, as inferred from the virtual endocasts in (**k**), left lateral; (**l**) dorsal views. Abbreviations: *a* ansate sulcus, *ar* anterior cebrebrum region, *cb* cerebellum plus brain stem region, *c* coronal sulcus, *cr* cruciate sulcus, *el* ectolateral sulcus, *es* ectosylvian sulcus, *l* lateral sulcus, *lf* longitudinal fissure, *pg* precruciate gyrus, *pr* posterior cerebrum region, *ps* presylvian sulcus, *s* sylvian sulcus, *ss* suprasylvian sulcus

IPS27340), it can be ascertained that the sylvian sulcus displays a curved (dorsally concave) contour, running from the frontobasal portion of the posterior region to the cerebrum, where it meets the presylvian sulcus. The ectosylvian sulcus is roughly parallel to the sylvian sulcus in all the studied specimens, with its dorsal end being slightly more curved frontally (Fig. 3a–c). The suprasylvian sulcus cannot be discerned along its entire course, although its two ends are well

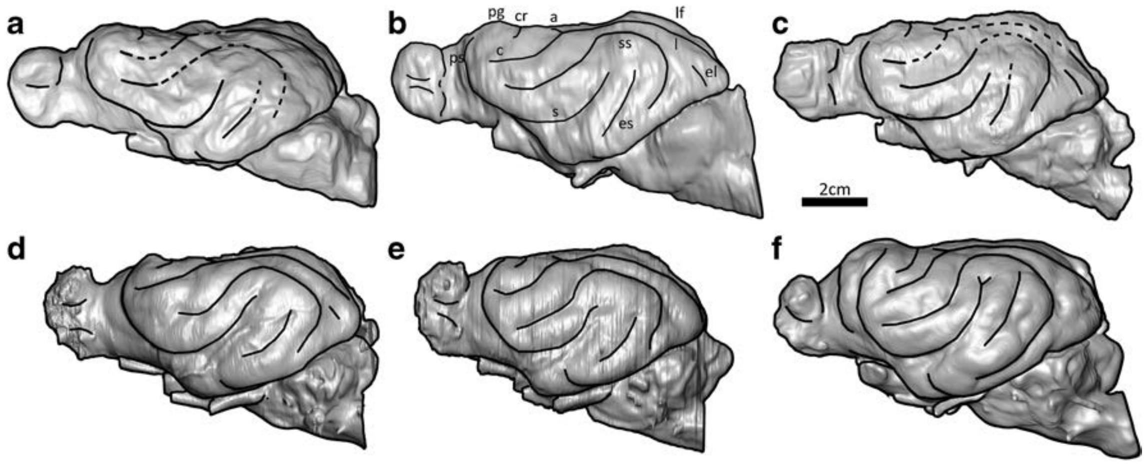

Fig. 3 Virtual endocasts of *Pliocrocuta perrieri* compared to those of extant bone-cracking hyaenids. (**a**), IPS36758; (**b**), IPS36759; (**c**), IPS27340; (**d**), *Parahyaena brunnea*; (**e**), *Hyaena hyaena*; (**f**), *Crocuta crocuta*. All specimens depicted in left lateral view. Endocasts for extant taxa derived from data taken from Digimorph.org. Abbreviations: *a* ansate sulcus, *ar* anterior region, *cb* cerebellum+brain stem region, *c* coronal sulcus, *cr* cruciate sulcus, *el* ectolateral sulcus, *es* ectosylvian sulcus, *l* lateral sulcus, *lf* longitudinal fissure, *pg* precruciate gyrus, *pr* posterior region, *ps* presylvian sulcus, *s* sylvian sulcus, *ss* suprasylvian sulcus

preserved; its caudal portion is markedly curved and parallel to the cerebrum-cerebellum "limit," whereas its frontal portion is much longer and almost parallel to the sylvian sulcus, more markedly curving to dorsal towards its frontal end. The coronal sulcus is preserved in IPS36759 and IPS27340 (only the frontal end), being also parallel to the suprasylvian sulcus, and joining in its posterior end the lateral and ansate sulci at a dorsal depression or "triple junction," near the longitudinal fissure (Fig. 3b). The lateral sulcus is parallel to the longitudinal fissure from the posterior region of the cerebrum to its mid area, when the former ends at the "triple junction." The ansate sulcus is partially preserved, starting at the dorsal depression or "triple junction," where the above-mentioned other sulci merge. The ectolateral sulcus is short and roughly parallel to the caudal region of the suprasylvian sulcus. The cruciate sulcus, although being hard to distinguish, is discernible in the three specimens, being located above the frontal end of the suprasylvian sulcus, anterior to the "triple junction" and posterior to the precruciate gyrus.

Frontal Sinus Comparisons

The presence in *Pliocrocuta* of craniocaudally elongated frontal sinuses that completely overlay the brain cavity resembles the condition displayed by extant bone-cracking hyenas (Fig. 1), whereas, in contrast, the insectivorous *Proteles cristatus* has a small frontal sinus that merely covers the area just below the frontal bone (Joeckel 1998). The frontal sinus of *Pliocrocuta* further resembles bone-cracking hyenas by showing a clear distinction between the anterior and posterior regions, and more specifically that of *Parahyaena* and, to a lesser extent, *Hyaena*, in the possession of outer convex walls, whereas *Crocuta* displays instead concave outer walls (Fig. 1). The frontal sinus of *Pliocrocuta* merely differs slightly from that of extant bone-cracking hyenas by the fact that its posterior portion is less simple, irregular, and asymmetric.

Among extinct hyaenids, elongated frontal sinuses have been documented in some late Miocene species (Joeckel 1998; Antón et al. 2006), such as *Adcrocuta eximia*, *Chasmaporthetes lunensis* Del Campana, 1914, *Ictitherium viverrinum* Roth and Wagner, 1854, *Palinhyaena reperta* Qiu, Huang, and Guo, 1979, and, especially, *Hyaenotherium wongii* Zdansky, 1924. However, no detailed description of the frontal sinuses was provided in the works cited above, so that they can be only compared to *Pliocrocuta* and the extant taxa regarding the length of the sinus and their percentage of overlap with the brain cavity. In particular, the bone-cracking hyena *Adcrocuta* displays elongated frontal sinuses that extend along the whole brain cavity or even further, thus reaching the nuchal crest. With regard to other taxa that are not bone-crackers, the sinuses of *Chasmaporthetes* are as elongated as those of *Adcrocuta*, whereas *Ictitherium* and *Hyaenotherium* possess somewhat less elongated frontal sinuses (which almost overlap the brain cavity), and only in *Palyinhyaena* the sinuses are much shorter and merely overlap 50–60 % of the brain cavity.

Brain Morphology Comparisons

Overall, *Pliocrocuta* displays a brain morphology and sulcal pattern similar to those of extant bone-cracking hyenas (Fig. 3), with more or less elongated olfactory bulbs, a variably expanded anterior cerebrum region (at the rostral cerebral fossa), and a trilobate cerebellum. There are, however, several differences compared to each of the extant taxa. Thus, *Pliocrocuta* displays a more elongated brain than the three extant bone-cracking hyenas, in accordance with the relatively longer and narrower cranium of the former. Such differences in brain elongation are more marked as compared to *Crocuta* and, to a lesser extent, *Hyaena* (which display a relatively shorter and rounder brain), and less so as compared to *Parahyaena* (in which the brain is nevertheless less elongated than in *Pliocrocuta*). The latter further resembles *Parahyaena* in displaying more anteriorly projected olfactory bulbs, thus differing in this regard from the condition of both *Crocuta* and *Hyaena*. Finally, *Pliocrocuta* resembles extant bone-cracking hyenas other than *Crocuta* in displaying an acuminated posterior contour of the brain, whereas in *Crocuta* the cerebellum is much more overlapped by the cerebrum.

With regard to the sulci, there are also several differences between *Pliocrocuta* and one or several of the living bone-cracking species. Thus, the curvature of the presylvian sulcus in the former is less extended dorsally than in the remaining taxa. The sylvian sulcus of *Pliocrocuta* displays, as in *Hyaena* and *Parahyaena*, a simple dorsal end, thus contrasting with the forked dorsal end present in *Crocuta.* In *Pliocrocuta*, the sylvian sulcus is less dorsally extended than in *Crocuta* and *Parahyaena*, thus resembling the condition observed in *Hyaena*. The anterior end of the coronal sulcus in *Pliocrocuta* is dorsally directed, as in *Hyaena* and *Parahyaena*, but differing from the more basally directed sulcus present in *Crocuta*. The curvature of the suprasylvian sulcus and its location relative to the ectosylvian sulcus in *Pliocrocuta* also more closely resemble the condition of *Hyaena* and *Parahyaena*, which differ from *Crocuta* in displaying a less abrupt curvature as well as more vertically aligned anterior and posterior borders. Similarly, the posterobasal end of the suprasylvian sulcus in *Pliocrocuta*, as in *Hyaena* and *Parahyaena*, is less basally extended than in *Crocuta*. Furthermore, the frontal end of the suprasylvian sulcus in *Pliocrocuta* displays a slight dorsal curvature, which is clearly distinguishable in *Parahyaena*, but absent in both *Crocuta* and *Hyaena*. Finally, in *Pliocrocuta* the cruciate sulcus is more anteriorly situated than in *Crocuta*, thus displaying a position similar to that in *Hyaena* and *Parahyaena*. To sum up, the disposition of the cruciate, suprasylvian, presylvian, and coronal sulci in *Pliocrocuta* more closely resembles the condition of *Hyaena* and *Parahyaena*, and shows more marked differences compared to *Crocuta*.

Encephalization and Anterior Cerebrum Relative Size

On the basis of the allometric regression of body mass vs. skull length derived in this paper for extant bone-cracking hyenas (Table 1), an estimated body mass of 56 kg (50 % confidence interval for the prediction: 54–58 kg) is computed from average cranial length in *P. perrieri*, with estimates for individual specimens ranging from 52 to 64 kg (see Table 2 for further details). The body mass inferred for *P. perrieri* is somewhat larger than in *C. crocuta*, which is the largest extant bone-cracking hyena (average body mass of 52 kg), in accordance to the longer cranium of *P. perrieri*. In contrast, the average total endocranial volume of *P. perrieri* (136 cm^3) is lower than in *C. crocuta* (160 cm^3), being intermediate between the latter and that of smaller extant bone-cracking hyenas (*H. hyaena* and *Pa. brunnea*; Table 3). This fact already indicates that *Pliocrocuta* is, at least to some degree, less encephalized than *Crocuta* (see below).

According to the results obtained from the allometric regression equations of encephalization (brain cavity volume vs. body mass; see Table 1 and Fig. 4a), extant felids and other feliforms display similar scaling relationships (with an allometric slope of 0.5), but the former are on average somewhat more encephalized—i.e., felids display an encephalization grade shift compared to most other feliforms. ANCOVA comparisons confirm that both groups do not differ in allometric slope (F=0.113, p=0.738), whereas in contrast significant differences are found in their respective intercepts (F=3,220.990, p<0.001). ANOVA comparisons of encephalization residuals between these two groups also indicate that such differences between felids and other feliforms are significant (F=4.943, p<0.05). With regard to hyaenids, *Proteles* falls just on the other feliforms regression (Fig. 4a), with a residual value similar to those of non-felid feliforms (Fig. 4b), even when the residuals for the latter are computed for the various included families separately (Tables 4 and 5). In contrast, felids display higher residual values on average (Fig. 4b and Table 5). The three extant bone-cracking hyenas, as well as all the specimens of *Pliocrocuta*, fall much closer to the felid regression (Tables 4 and 5; Fig. 4b), with *Crocuta* and, to a lesser extent, *Hyaena*, falling even somewhat above the felid regression. This indicates that, like felids, extant bone-cracking hyenas are more encephalized than most other feliforms (including *Proteles*). The degree of encephalization of *Pliocrocuta*, as far as it can be ascertained on the basis of the three available specimens, appears most similar to *Parahyaena*, i.e., somewhat lower than in *Hyaena* and, especially, *Crocuta*, although being comparable to the average felid condition and further being clearly higher than in *Proteles* and other (non-felid and non-hyaenid) extant feliforms (Fig. 4b; Tables 4 and 5).

With regard to regional volumes in the three available specimens (Table 3), *Pliocrocuta* displays a smaller anterior cerebrum region (16 cm^3) than all extant bone-cracking hyenas, especially as compared to *Crocuta* (39 cm^3), in spite of the fact that these two genera display similarly-sized posterior cerebrum regions (87 vs. 91 cm^3, respectively). As a result, the size of the anterior cerebrum region relative to total endocranial volume in *Pliocrocuta* is rather small (11 %; see Table 3 and Fig. 5), being most similar to the condition in *Proteles* (10 %), and much smaller than in *Hyaena* (17 %), *Parahyaena* (18 %), and, especially, *Crocuta* (25 %). The size of the posterior cerebrum region relative to total endocranial

Table 1 Allometric regressions derived in this paper for assessing relative brain size (encephalization) as well as for estimating body mass

Group								Slope			Intercept	
	log Y	log X	N	r	p	SEE	Slope	95 % CI		Intercept	95 % CI	
Felids	log ECV	log BM	24	0.983	<0.001	0.057	0.526	0.482	0.570	1.189	1.133	1.245
Other feliforms	log ECV	log BM	42	0.921	<0.001	0.086	0.512	0.443	0.581	1.062	1.027	1.096
Bone-cracking hyenas	log BM	log SKL	3	0.998	<0.05	0.010	9.183	2.404	15.961	-19.752	35.510	-3.994

Abbreviations: *BM* body mass (in kg), *CI* confidence interval, *ECV* total endocranial volume (in mm^3), *N* sample size, *p* significance, *SEE* standard error of estimate, *r* correlation coefficient, *SKL* skull length, *X* independent variable, *Y* dependent variable

volume in *Pliocrocuta* (64 %; see Table 3 and Fig. 5) is also essentially comparable to *Proteles* (63 %), being slightly higher than in *Hyaena* (61 %) and *Parahyaena* (60 %), and especially compared with *Crocuta* (57 %). When the whole volume of the cerebrum is considered, that of *Pliocrocuta* (103 cm^3) is intermediate between those of *Crocuta* (130 cm^3) and *Parahyaena* (86 cm^3) in absolute terms. Regarding the ratio between total cerebrum volume and total brain cavity volume, *Pliocrocuta* (76 %) is virtually indistinguishable from both *Hyaena* and *Parahyaena* (Table 3 and Fig. 5), whereas in contrast *Crocuta* displays a somewhat higher value (81 %) and *Proteles* a smaller one (73 %). Finally, the volume of the cerebellum plus brain stem region in *Pliocrocuta* (28 cm^3) is more similar to that of *Crocuta* (26 cm^3), and larger than in *Parahyaena* (21 cm^3). However, in relative terms, this region in *Pliocrocuta* (20 %) is larger than in extant bone-cracking hyaenas (Table 3 and Fig. 5), including not only *Parahyaena* (19 %) and *Hyaena* (18 %), but especially *Crocuta* (17 %), although smaller than in *Proteles* (23 %).

Table 2 Body mass estimates for *Pliocrocuta perrieri* and extant bone-cracking hyenas (based on an allometric regression of mean species values for extant bone-cracking hyaenids)

Species	SKL	BM	BME	50 % CI		% PE
Crocuta crocuta	217.91	51.96	52.47	50.82	54.22	-0.98
Parahyaena brunnea	211.36	40.45	39.65	38.58	40.78	2.02
Hyaena hyaena	204.46	28.97	29.23	28.30	30.21	-0.90
Pliocrocuta perrieri (IPS36758)	218.47	-	53.75	51.99	55.56	-
Pliocrocuta perrieri (IPS36759)	222.76	-	64.25	61.75	66.86	-
Pliocrocuta perrieri (IPS27340)	217.64	-	51.90	50.26	53.59	-
Pliocrocuta perrieri (mean)	219.62	-	56.40	54.47	58.40	-

Abbreviations: *BM* body mass (in kg), *BME* body mass estimate (in kg), *CI* confidence interval for the prediction of BME, *PE* prediction error (%), computed as (BME-BM)/BME*100, *SKL* skull length (in mm)

BME was computed on the basis of the allometric regression of log BM vs. log SKL reported in Table 1

Discussion

Functional Implications of Frontal Sinus Morphology

The elongated frontal sinus of *Pliocrocuta* most closely resembles that of extant bone-cracking hyaenas and differs from the condition displayed by the insectivorous *Proteles*, although similarly elongated frontal sinuses have been further documented in other, non-bone-cracking Miocene hyaenids. The latter fact suggests that elongated frontal sinuses, very uncommon among carnivorans, probably originated very early in the evolutionary history of the Hyaenidae. The elongated frontal sinuses of the above-mentioned Miocene species, however, never attain the degree of caudal extension displayed by extant bone-cracking hyenas, in which the sinuses completely overlay the brain cavity (Joeckel 1998). In this regard, our study shows that the posteriorly-elongated frontal sinuses of *Pliocrocuta* completely overlap the brain cavity (Fig. 2a), thus most closely resembling the condition of extant bone-cracking taxa than that of the above-mentioned extinct hyaenids. Among fossil hyaenids, the condition of extant bone-cracking hyenas had been only previously reported for the late Miocene *Adcrocuta* (Joeckel 1998) and the hunting hyena *Chasmaporthetes lunensis* (Antón et al. 2006; Tseng et al. 2011).

Overall, the customary attribution of both *Pliocrocuta* and *Adcrocuta* to the bone-cracking morphotype (based on dental morphology, see discussion in Turner et al. (2008) is further supported by the morphology of the frontal sinuses in these taxa. A functional relationship between bone-cracking habits and caudally elongated frontal sinuses (and associated vaulted foreheads) would be further supported by the fact that such a morphology is very rare among other carnivorans, being only displayed by several extinct borophagine canids from the Neogene and Quaternary of North America, which are also inferred to have been opportunist scavengers with bone-cracking adaptations (Werdelin 1989), although several controversies exist about their feeding behavior (Van Valkenburgh et al. 2003; Andersson 2005). It should be however taken into account that, in these canids, the frontal sinus is not as posteriorly extended as in extant bone-cracking hyenas (Werdelin 1989; Joeckel 1998).

Table 3 Total and regional endocranial volumes in *Pliocrocuta perrieri*, compared to mean species values for extant hyaenids

Species	ECV	ACV	PCV	CV	CSV	RAC	RPC	RC	RCS
Crocuta crocuta	160058.94	39181.02	90882.65	130063.67	26474.06	0.245	0.568	0.813	0.165
Parahyaena brunnea	111010.33	19624.81	66813.21	86438.02	21025.3	0.177	0.602	0.779	0.189
Hyaena hyaena	104114.17	17601.17	63953.03	81554.2	19004.23	0.169	0.614	0.783	0.183
Proteles cristatus	38105.87	3742.81	23887.75	27630.56	8702.96	0.098	0.627	0.725	0.228
Pliocrocuta perrieri (IPS36758)	130053.98	15598.09	85246.10	100844.19	24959.62	0.120	0.655	0.775	0.191
Pliocrocuta perrieri (IPS36759)	146107.56	17103.26	92070.64	109176.91	32813.81	0.117	0.630	0.747	0.225
Pliocrocuta perrieri (IPS27340)	132446.87	16164.89	83411.79	99576.68	25542.35	0.122	0.630	0.752	0.193
Pliocrocuta perrieri (mean)	136191.39	16289.75	86909.51	103199.26	27771.85	0.112	0.638	0.758	0.204

Abbreviations: *ACV* anterior cerebrum volume (in mm^3), *CSV* cerebellum plus brain stem volume (in mm^3), *CV* total cerebrum volume (in mm^3), *ECV* total endocranial volume (in mm^3), *PCV* posterior cerebrum volume (in mm^3), *RAC* relative anterior cerebrum volume (computed as ACV / ECV), *RCS* relative cerebellum plus brain stem volume (computed as CSV / ECV), *RC* relative cerebrum volume (computed as CV/ECV), *RPC* relative posterior cerebrum volume (computed as PCV / ECV). Data for extant taxa taken from Sakai et al. (2011)

The function of expanded and elongated frontal sinuses among carnivorans is however unclear to a large extent. Functional hypotheses, variously relating this morphology to either shock dissipation, brain cooling, olfaction, or maximization of muscle attachment areas, have been proposed by several authors, although most of these explanations are not entirely satisfactory (see review in Joeckel 1998). Thus, Werdelin (1989) has related the vaulted foreheads and large frontal sinuses of borophagines and bone-cracking hyenas to the need to dissipate the high compressive forces generated by premolar bone-cracking. However, as previously noted (Joeckel 1998), the bone-cracking diet of these taxa may only explain the anterior enlargment of the frontal sinus, but not the posterior elongation displayed by *Adcrocuta*, *Crocuta*, *Hyaena,* and *Parahyaena*. Following Joeckel's (1998) interpretation, the elongated frontal sinuses and associated cranial pneumatization displayed by these hyaenids would provide increased resistance to the various stresses imposed on the skull (not necessarily due to masticatory muscles forces), by acting as a buttress between the neurocranium and the splanchnocranium, and thereby resisting any dorsal torque imposed on the face during biting. This hypothesis has been tested in a work involving finite elements analysis in *Crocuta crocuta* (Tanner et al. 2008), which shows that the development of this feature slightly improves the biomechanical performance of the skull when dispersing stresses from the forehead to the sagittal region. Also, a similar work focused on *Chasmaporthetes lunensis* has recently proposed that this feature would allow this species to behave as an almost fully-developed bone-cracker in terms of durophagy (Tseng et al. 2011), being only slightly less efficient with regard to the dissipation of bite stresses.

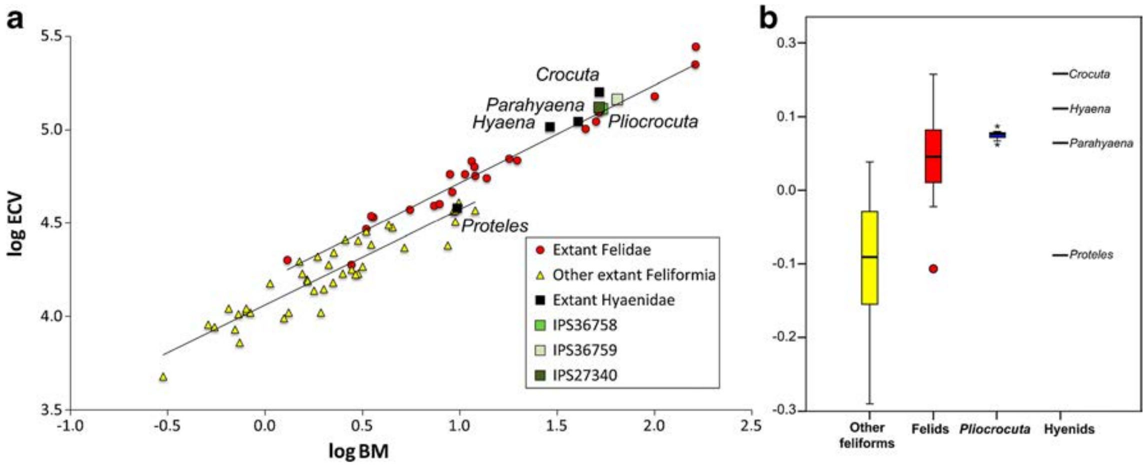

Fig. 4 Encephalization in *Pliocrocuta*, compared with extant hyaenids and other feliform carnivorans. (**a**), Allometric regressions of encephalization, i.e., total endocranial volume vs. body mass, separately for hyaenids, felids, and other feliform canivorans. (**b**), Boxplots showing the differences between these groups in encephalization residuals (based on the other feliform regression); the *Pliocrocuta* boxplot is based on encephalization residuals computed for each specimen (based on their respective estimated body masses), whereas the two extreme values denoted by asterisks correspond to maximum and minimum residuals computed for this sample based on the 50 % confidence intervals for the predictions of the estimated body mass for each individual (see Table 4). See Materials and methods for data sources. Abbreviations: *BM* body mass (in kg), *ECV* total endocranial volume (in mm^3)

Table 4 Encephalization residuals for *Pliocrocuta* compared with those for extant hyaenids. See Table 4 for descriptive statistics of encephalization residuals in other feliform families

Taxon	Mean
Crocuta crocuta	0.258
Parahyaena brunnea	0.164
Hyaena hyaena	0.211
Proteles cristatus	0.012
Pliocrocuta perrieri (IPS36758)[a]	0.167 (0.162–0.172)
Pliocrocuta perrieri (IPS36759)[a]	0.177 (0.166–0.187)
Pliocrocuta perrieri (IPS27340)[a]	0.180 (0.175–0.190)
Pliocrocuta perrieri (mean)[a]	0.176 (0.165–0.184)

[a] The ranges reported for *Pliocrocuta perrieri* correspond to the encephalization residuals computed taking into account the 50 % CI for the body mass estimates (see Table 2)

Encephalization residuals were computed on the basis of the other feliforms regression line of endocranial volume vs. body mass reported in Table 1

To sum up, the morphology of the frontal sinuses displayed by *Pliocrocuta* provides additional evidence supporting a bone-cracking ecomorphotype for this extinct taxon. However, biomechanical analyses would be required to further clarify the functional significance of the morphology shared between *Pliocrocuta* and other bone-cracking taxa. Additional research on extinct hyaenids attributed to other ecomorphotypes would be further required to confirm the adaptive significance hypothesized above for their completely elongated sinuses.

Phylogenetic Implications of Brain Morphology

It is generally considered that extinct bone-cracking hyenas are more closely related to *Crocuta* than to either *Hyaena* or *Parahyaena* (Werdelin and Solounias 1991; Turner et al. 2008). Such a phylogenetic hypothesis, which is mainly based on dentognathic features, has been traditionally advocated by several authors (Gaudry 1862–1867; Schlosser 1890; Pilgrim 1932; Howell and Petter 1980). Some other authors, however, have sometimes dissented, by suggesting that *Pliocrocuta* might be alternatively more closely related to *Hyaena* and *Parahyaena* (Thenius 1966; Kurtén 1968). The comparisons of internal cranial morphology performed in this paper rather support the latter hypothesis, because the brain morphology and sulcal pattern of the studied specimens most closely resemble those of *Hyaena hyaena* and *Parahyaena brunnea*, instead of those of *Crocuta crocuta*.

Table 5 Descriptive statistics of encephalization residuals in non-hyaenid feliform families

Taxon	N	Mean	SD	95 % CI		Range	
Felidae	24	0.144	0.056	0.120	0.168	-0.007	0.257
Eupleridae	5	0.020	0.089	-0.090	0.130	-0.077	0.136
Herpestidae	19	-0.006	0.097	-0.052	0.041	-0.190	0.139
Viverridae	16	0.001	0.077	-0.040	0.042	-0.163	0.106
Prionodontidae	2	-0.04	0.072	-0.650	0.642	-0.055	0.047

Abbreviations: *CI* confidence interval, *N* sample size, *SD* standard deviation

Encephalization residuals were computed on the basis of the other feliforms regression line of endocranial volume vs. body mass reported in Table 1

However, on the basis of the information provided by the extant taxa and *Pliocrocuta* alone it is not possible to confidently discount the possibility that the similarities in brain morphology between this taxon and both *Hyaena* and *Parahyaena* are merely symplesiomorphies, i.e., primitive retentions that would not necessarily indicate a closer relationship between these taxa. Alternatively, *Crocuta* and *Pliocrocuta* mighy be more closely related to each other if the divergent brain morphology of the former postdated the split with the lineage leading to *Pliocrocuta*. Additional research on the internal cranial morphology of other bone-cracking extinct hyenas would be therefore required to establish the polarity of the discussed characters and, hence, more confidently discuss their phylogenetic implications.

Behavioral Inferences

For extinct hyaenids, paleobiological inferences on social behavior and feeding strategies have been made for some taxa on the basis of taphonomical studies on bone accumulations (Turner and Antón 1996)—i.e., the putative dens of *Pachycrocuta brevirostris* in Venta Micena (Spain; Palmqvist et al. 2011) and Zhoukoudian 1 (China; Boaz et al. 2000). Some other studies have relied on encephalization metrics (relative brain size) to infer social behavior on fossil carnivorans in general (Finarelli and Flynn 2009) or extant hyaenids in particular (Sakai et al. 2011), but no study has previously focused on an extinct hyaenid such as *Pliocrocuta*.

Brains are metabolically very expensive organs, so that significant selective advantages are expected towards the evolution of large brains (Dunbar 1998). In primates, a relationship between sociality and encephalization has been recognized for several decades (Byrne and Whiten 1988), being articulated around the "social brain hypothesis" (SBH; Barton and Dunbar 1997; Dunbar 1998, 2003). Originally proposed for primates, this hypothesis argues that individuals living in stable social groups must confront higher cognitive demands than those living alone or in unstable aggregations, so that the information-processing capacity of the brain would consequently constrain group size (Barton and Dunbar 1997; Dunbar and Shultz 2007a). More recent refinements of the SBH have emphasized that the relationship between brain size (or neocortex size) and group size is quite complex, but have tended to confirm a

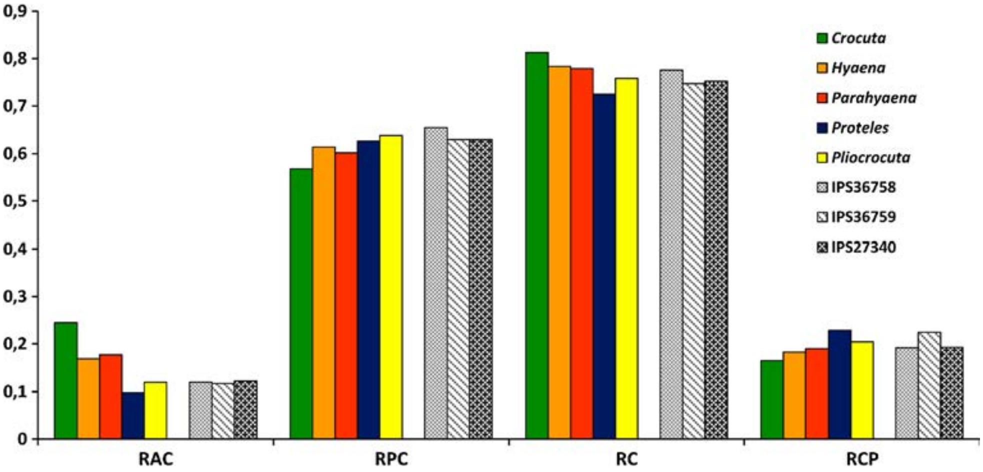

Fig. 5 Histograms of relative regional brain volumes in *Pliocrocuta perrieri*, compared to extant hyaenids. See Table 3 for numerical results. Abbreviations: *RAC* relative anterior cerebrum volume, *RC* relative cerebrum volume, *RCS* relative cerebellum plus brain stem volume, *RPC* relative posterior cerebrum volume. Data for extant taxa taken from Sakai et al. (2011)

relationship with social complexity (Dunbar and Shultz 2007a; Shultz and Dunbar 2010), or at least with some of its aspects, such as pair-bonding (Dunbar and Shultz 2007b).

There have been several attempts to extend the SBH to non-primate taxa, including, among other groups, carnivorans (Dunbar and Bever 1998; Pérez-Barbería et al. 2007). Pérez-Barbería et al. (2007) have confirmed that there is a significant relationship between relative brain size and social complexity, but have further noted that carnivorans are especially prone to decoupling these two factors in the course of evolution. Finarelli and Flynn (2009) have further argued that the relationship between social complexity and increased encephalization in carnivorans as a whole is exclusively dependent on the inclusion of the social canids, whereas no relationship would exist among the remaining taxa (including hyaenids). The latter conclusion, however, has been subsequently disputed by Shultz and Dunbar (2010), who stressed again the role of sociality in the evolutionary increase in encephalization.

An analysis focused on extant hyaenids (Sakai et al. 2011), following a research line initiated by Holekamp and coauthors (Holekamp et al. 2007a, b), established a positive correlation between the relative size of the anterior brain and group size—with the most social *Crocuta* displaying the greatest development of this region, and the solitary *Proteles* the least. Besides several other structures (such as the ventral pallidum, the olfactory tubercle, the prepiriform cortex, and a small portion of the most rostral head of the caudate nucleus), the anterior region of the brain is mainly constituted by the frontal cortex. In primates and other mammals, the frontal cortex intervenes in complex cognitive processes related to social decision-making (Adolphs 2001; Amodio and Frith 2006), such as the inhibitory behaviors required in complex fission-fusion societies. Therefore, a relatively larger frontal cortex may reflect the enhanced abilities required to process social information (Sakai et al. 2011).

To further verify these hypotheses, and in the direction of the previous works, a recent study (Swanson et al. 2012) has been performed in carnivorans as a whole, by relying on total and regional brain volumes, to test their correlation with some behavioral variables. Some conclusions of this study are that, although there is no support for a role of social complexity in overall encephalization amongst carnivorans, relative brain region sizes are correlated with sociality. In particular, cerebrum volume would be positively correlated with sociality, whereas the cerebellum plus brain stem volume would be inversely correlated with complex sociality. Swanson et al. (2012) have also made several inferences about the relationship between brain proportions and both home range and forelimb usage (related to foraging strategies), concluding that relative anterior brain volume is inversely correlated with both of them.

Our study shows that the extinct hyaenid *P. perrieri*, with a smaller brain but a somewhat higher estimated body mass than *Crocuta*, displays a degree of encephalization intermediate between that of the solitary *Proteles* and the very gregarious *Crocuta*, thus being most comparable in this regard to the intermediate condition of *Parahyaena*. Moreover, *Pliocrocuta* displays a relatively small anterior cerebrum region, comparable to the condition shown by *Proteles*, and a cerebrum and cerebellum comparable in size to those of *Hyaena* and *Parahyaena*. These results are in agreement with the brain morphology and sulcal pattern of *Pliocrocuta*, which as discussed above are more similar to those of *Hyaena* and *Parahyaena* than to those of *Crocuta*. On the other hand, and taking into account previous considerations in this regard (Sakai et al. 2011; Swanson et al. 2012), the development of the anterior region, the whole cerebrum (anterior plus posterior), and the cerebellum of *Pliocrocuta* suggest for this taxon a less complex social behavior than in extant *Crocuta*, and thus more similar to that of *Parahyaena* and *Hyaena* (although maybe slightly less complex).

Several aspects of social behavior, including gregariousness, hunting abilities, territoriality and foraging strategies, are closely linked, so that in absence of taphonomical evidence it seems difficult to conclusively refine our inference above that *Pliocrocuta* displayed a less complex social behavior than *Crocuta*. However, it should be taken into account that extant bone-cracking hyaenids show in these regards different strategies. Thus, whereas *Crocuta* is an active pack-hunter (Kruuk 1972; Cooper et al. 1999), both *Hyaena* and *Parahyaena* are basically scavengers, although they can also hunt small prey alone (Kruuk 1972; Mills 1990; Wagner 2006). These differences in foraging strategies are also related to differences in locomotion and home range. In particular, *Crocuta* displays larger home ranges (from 40 km^2 up to 1, 000 km^2; Kruuk 1972; Mills 1990) as well as more complex territorial behaviors (including territory marking, boundaries patrolling, etc; Mills 1990) than both *Parahyaena* and *Hyaena*. Moreover, although foraging strategies are very variable within each taxon, *Crocuta* generally travels greater distances from the core area of the clan's range in search for prey (30–40 km or more; Eloff 1964; Tilson and Henschel 1986) than either *Parahyaena* or *Hyaena*, which travel between 20 and 50 each night looking for carcasses and other kinds of food (Kruuk 1976; Mills 1990). The inverse correlation previously noted by Swanson et al. (2012) between anterior cerebrum volume and both home range and forelimb usage suggests that *Pliocrocuta* was more comparable in these regards to *Parahyaena* and *Hyaena*, thereby probably displaying a more restricted home range and a less pronounced forelimb usage than *Crocuta*.

Conclusions

We describe for the first time the internal cranial anatomy of an extinct hyaenid (*Pliocrocuta perrieri*), including not only the frontal sinuses but also the brain morphology, based on three crania from the late Pliocene of Villarroya and the early Pleistocene of La Puebla de Valverde (Iberian Peninsula). Our results indicate that this species displays posteriorly elongated frontal sinuses that completely overlap the brain cavity. This condition, unambiguously documented only in extant bone-cracking hyenas and in the extinct bone-cracking hyaenid *Adcrocuta*, therefore confirms that *Pliocrocuta* likely displayed bone-cracking habits (as previously inferred on the basis of dental morphology). We further show that the brain morphology of *Pliocrocuta*, as far as it can be ascertained on the basis of its virtual endocast, is more similar to those of *Hyaena hyaena* and *Parahyaena brunnea* than to that of *Crocuta crocuta*. Similarities with the two former species of extant hyaenids include not only the brain sulcal pattern (shape and position of the cruciate, coronal, and presylvian sulci, among other features), but also the moderate degree of encephalization (lower than in *Crocuta*). From a paleobiological viewpoint, the poor development of the anterior cerebrum, the moderate development of the cerebrum, and the high development of the cerebellum plus the brain stem of *Pliocrocuta* reported in this paper suggest that this taxon probably displayed a less complex social behavior than extant bone-cracking hyenas, especially compared to *Crocuta*. More specifically, and based on the relative size of the anterior cerebrum, it is likely that these differences were further related to differences in foraging strategies, with *Pliocrocuta* being more comparable in home range and forelimb usage to *Hyaena* and *Parahyaena*, and probably lacking the complex pack-hunting and territorial behaviors of *Crocuta*. To a large extent, these inferences rely on the validity of the correlations previously established by other authors between total and regional brain volumes and social behavior in extant taxa. Accordingly, additional research on the functional basis of such correlations in extant hyaenids would be required to further test the validity of the paleobiological inferences on social behavior and foraging strategy made in this paper.

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References

Adolphs R (2001) The neurobiology of social cognition. Curr Opin Neurobiol 11: 231–239. doi: 10.1016/S0959-4388(00)00202-6

Agustí J, Oms O (2001) On the age of the last hipparionine faunas in western Europe. C R Acad Sci Paris 332: 291–297. doi: 10.1016/S1251-8050(01)01523-3

Alba DM (2010) Cognitive inferences in fossil apes (Primates: Hominoidea): does encephalization reflect intelligence? J Anthropol Sci 88: 11–48

Amodio DM, Frith CD (2006) Meeting of minds: the medial frontal cortex and social cognition. Nat Rev Neurosci 7: 268–277. doi: 10.1038/nrn1884

Anadón P, Utrilla R, Vázquez A, Martín-Rubio M, Rodriguez-Lázaro J, Robles F (2009) Paleoenviromental evolution of the Pliocene Villarroya lake, northern Spain, from stable isotopes and trace-element geochemistry of ostracods and mollusks. J Paleolimnol 39: 339–419. doi: 10.1007/s10933-007-9121-2

Andersson J (2005) Were there pack-hunting canids in the Tertiary, and how can we know? Paleobiology 31: 56–72

Antón M, Turner A, Salesa MJ, Morales J (2006) A complete skull of *Chasmaporthetes lunensis* (Carnivora, Hyaenidae) from the Spanish Pliocene site of La Puebla de Valverde (Teruel). Estudios Geol 62: 375–388. doi: 10.3989/egeol.0662132

Arribas Herrera A, Bernad García J (1994) Catálogo de mamíferos pliocenos del yacimiento de Villarroya (La Rioja), en la colección del Museo Geominero. Bol Geol Min 105: 236–248

Arsznov BM, Lundrigan BL, Holekamp KE, Sakai ST (2010) Sex and the frontal cortex: a developmental CT study in the spotted hyena. Brain Behav Evol 76: 185–97. doi: 10.1159/000321317

Barton RA, Dunbar RIM (1997) Evolution of the social brain. In: Whiten A, Byrne R (eds) Machiavellian Inteligence II. Cambridge Unversity Press, Cambridge, pp 240–263

Boaz NT, Ciochon RL, Xu Q, Liu J (2000) Large mammalian carnivores as a taphonomic factor in the bone accumulation at Zhoukoudian. Acta Anthropol Sinica 19: 224–234

Byrne R, Whiten A (1988) Machiavellian Intelligence. Oxford University Press, Oxford

Cooper SM, Holekamp KE, Smale L (1999) A seasonal feast: long-term analysis of feeding behavior in the spotted hyaena *Crocuta crocuta* (Erxbelen). Afr J Ecol 1: 178–180

Crusafont Pairó M, Hartenberger JL, Heintz E (1964) Un nouveau gisement de Mammifères fossiles d'âge villafranchien à La Puebla de Valverde (Province de Teruel, Espagne). C R Hebd Séances Acad Sci 258: 2869–2871

Dockner M (2006) Comparisons of *Crocuta crocuta crocuta* and *Crocuta crocuta spelaea* through computer tomography. M.S. Dissertation, University of Vienna

Dunbar RIM (1998) The social brain hypothesis. Evol Anthropol 6: 178–190. doi: 10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8

Dunbar RIM (2003) The social brain: mind, language, and society in evolutionary perspective. Annu Rev Anthropol 32: 163–181. doi: 10.1146/annurev.anthro.32.061002.093158

Dunbar RIM, Bever J (1998) Neocortex size predicts group size in carnivores and some insectivores. Ethology 104: 695–708. doi: 10.1111/j.1439-0310.1998.tb00103.x

Dunbar RIM, Shultz S (2007a) Understanding primate brain evolution. Phil Trans R Soc B 362: 649–658. doi: 10.1098/rstb.2006.2001

Dunbar RIM, Shultz S (2007b) Evolution in the social brain. Science 317: 1344–1347. doi: 10.1126/science.1145463

Eloff FC (1964) On the predatory habits of lions and hyaenas. Koedoe 7: 105–112

Finarelli JA, Flynn JJ (2009) Brain-size evolution and sociality in Carnivora. Proc Natl Acad Sci USA 106: 345–349. doi: 10.1073/pnas.0901780106

Gaudry A (1862–1867) Animaux Fossiles du Mont Leberon. F. Savy, Paris, pp 475

Gautier F, Heintz E (1974) Le gisement villafranchien de La Puebla de Valverde (Province de Teruel, Espagne). Bull Mus Natl Hist Nat 36: 113–133

Gould SJ (1966) Allometry and size in ontogeny and phylogeny. Biol Rev 41: 587–640. doi: 10.1111/j.1469-185X.1966.tb01624.x

Gould SJ (1975) Allometry in primates, with emphasis on scaling and the evolution of the brain. Contrib Primatol 5: 244–292

Holekamp KE, Sakai ST, Lundrigan BL (2007a) Social intelligence in the spotted hyena (*Crocuta crocuta*). Phil Trans R Soc Lond B 362: 523–538. doi: 10.1098/rstb.2006.1993

Holekamp KE, Sakai ST, Lundrigan BL (2007b) The spotted hyena (*Crocuta crocuta*) as a model system for study of the evolution of intelligence. J Mammal 88: 545–554. doi: 10.1644/06-MAMM-S-361R1.1

Howell FG, Petter G (1980) The *Pachycrocuta* and *Hyaena* lineages (Plio-Pleistocene and extant species of the Hyaenidae). Their relationships with Miocene ictitheres: *Palhyaena* and *Hyaenictitherium*. Geobios 13: 579–623. doi: 10.1016/S0016-6995(80)80004-0

Jerison HJ (1973) Evolution of the Brain and Intelligence. Academic Press, New York

Jiménez García S, Martín de Jesús S, Jiménez Fuentes E (1999) Primeros resultados de la excavación "Villarroya 88-89". Stvdia Geológica Salmanticensia 35: 41–56

Joeckel RM (1998) Unique frontal sinuses in fossil and living Hyaenidae (Mammalia, Carnivora): description and interpretation. J Vertebr Paleontol 18: 627–639. doi: 10.1080/02724634.1998.10011089

Klingenberg CP (1998) Heterochrony and allometry: the analysis of evolutionary change in ontogeny. Biol Rev 73: 79–123. doi: 10.1111/j.1469-185X.1997.tb00026.x

Kruuk H (1972) The Spotted Hyena: Study of Predation and Social Behavior. Chicago University Press, Chicago

Kruuk H (1976) Feeding and social behavior of the striped hyaena (*Hyaena hyaena* Desmarest). E Afr Wildl J 4: 91–111

Kurtén B (1968) Pleistocene Mammals of Europe. Weidenfeld and Nicolson, London

Martin RD, Barbour AD (1989) Aspects of line-fitting in bivariate allometric analyses. Folia Primatol 53: 65–41. doi: 10.1159/000156409

Mills MGL (1990) Kalahari Hyaenas: The Comparative Behavioral Ecology of Two Species. Unwin Hyman, London

Palmqvist P, Martínez-Navarro B, Pérez-Claros JA, Torregrosa V, Figueirido B (2011) The giant hyena *Pachycrocuta brevirostris*: modelling the bone-cracking behavior of an extinct carnivore. Quaternary Internatl 243: 61–79. doi: 10.1016/j.quaint.2010.12.035

Paulli S (1900) Über die Pneumaticität des Schädels bei den Säugethieren. III. Über die Morphologie des Siebbeins und die der Pneumaticität bei den Insectivoren, Hyracoideen, Chiroptera, Carnivoren, Pinnipedien, Edentaten, Prosimiern und Primaten. Gegenbaurs Morphol Jahrb 28: 483–564

Pérez-Barbería FJ, Shultz S, Dunbar RIM (2007) Evidence for coevolution of sociality and relative brain size in three orders of mammals. Evolution 61: 2811–2821. doi: 10.1111/j.1558-5646.2007.00229.x

Pilgrim GE (1932) The fossil Carnivora of India. Paleontol Indica 18: 1–232

Radinsky L (1971) An example of parallelism in carnivore brain evolution. Evolution 25: 518–522

Radinsky L (1975) Evolution of the felid brain. Brain Behav Evol 11: 214–253. doi: 10.1159/000123636

Radinsky L (1977) Brains of early carnivores. Paleobiology 3: 333–349

Sakai ST, Arsznov BM, Lundrigan BL, Holekamp KE (2011) Brain size and social complexity: a computed tomography study in Hyaenidae. Brain Behav Evol 77: 91–104. doi: 10.1159/000323849

Schlosser M (1890) Die Aven, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des europäischen Tertiärs. III. Beitr Paläontol Geol Osterr Ung 8: 1–107

Shultz S, Dunbar R (2010) Encephalization is not a universal macroevolutionary phenomenon in mammals but is associated with sociality. Proc Natl Acad Sci USA 107: 21582–21586. doi: 10.1073/pnas.1005246107

Sinusía C, Pueyo EL, Azanza B, Pocoví A (2004) Datación magnetoestratigráfica del yacimiento paleontológico de Puebla de Valverde (Teruel). GeoTemas 6: 339–342

Smith RJ (1984) Determination of relative size: the "criterion of subtraction" problem in allometry. J Theor Biol 108: 131–142. doi: 10.1016/S0022-5193(84)80174-5

Swanson EM, Holekamp KE, Lundrigan BL, Arsznov BM, Sakai ST (2012) Multiple determinants of whole and regional brain volume among terrestrial carnivorans. PLoS ONE 7: e38447. doi: 10.1371/journal.pone.0038447

Tanner JB, Dumont ER, Sakai ST, Lundrigan BL, Holejamp KE (2008) Of arcs and vaults: the biomechanics of bone-cracking in spotted hyenas (*Crocuta crocuta*). Biol J Linn Soc 95: 246–255. doi: 10.1111/j.1095-8312.2008.01052.x

Thenius E (1966) Zur Stammegeschichte der Hyänen (Carnivora, Mammalia). Z Säugetierk 31: 293–300

Tilson RL, Henschel JR (1986) Spatial arrangement of spotted hyaena groups in a desert envoiroment, Namibia. Afr J Ecol 4: 173–180

Tseng ZJ, Antón M, Salesa MJ (2011) The evolution of the bone-cracking model in carnivorans: cranial functional morphology of the Plio-Pleistocene cursorial hyaenid *Chasmaporthetes lunensis* (Mammalia: Carnivora). Paleobiology 37: 140–156. doi: 10.1666/09045.1

Turner A, Antón M (1996) The giant hyaena *Pachycrocuta brevirostris* (Mammalia, Carnivora, Hyaenidae). Geobios 29: 455–468. doi: 10.1016/S0016-6995(96)80005-2

Turner A, Antón M, Werdelin L (2008) Taxonomy and evolutionary patterns in the fossil Hyaenidae of Europe. Geobios 41: 677–687. doi: 10.1016/j.geobios.2008.01.001

Van Valkenburgh B (1990) Skeletal and dental prefictors of body mass in carnivores. In: Damuth J, MacFadden B (eds) Body Size in Mammalian Paleobiology: Estimation and Biological Implications. Cambridge University Press, Cambridge, pp 181–205

Van Valkenburgh B, Sacco T, Wang X (2003) Pack hunting in Miocene borophagine dogs: evidence from craniodental morphology and body size. Bull Am Mus Nat His 13: 147–162

Vinuesa V, Madurell-Malapeira J, Ansón M, Alba DM (2014) New cranial remains of *Pliocrocuta perrieri* (Carnivora, Hyaenidae) from the Villafranchian of the Iberian Peninsula. Boll Soc Paleont Ital 53: 39–47

Wagner AP (2006) Behavioral ecology of the striped hyaena (*Hyaena hyaena*). Ph.D. Dissertation, Montana State University

Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. Biol Rev 81: 259–291. doi: 10.1017/S1464793106007007

Werdelin L (1989) Constraint and adaption in the bone-cracking canid *Osteoborus* (Mammalia: Canidae). Paleobiology 15: 387–401

Werdelin L, Solounias N (1991) The Hyaenidae: taxonomy, systematics and evolution. Fossils Strata 30: 1–104

Werdelin L, Solounias N (1996) The evolutionary history of hyenas in Europe and western Asia during the Miocene. In: Bernor RL, Fahlbusch R, Mittmann HW (eds) The Evolution of Western Eurasian Neogene Mammal Faunas. Columbia University Press, New York, pp 290–306

Werdelin L, Turner A (1996a) The fossil and living Hyaenidae of Africa: present status. In: Stewart KM, Seymour KL (eds) Palaeoecology and Palaeoenvironments of Late Cenozoic Mammals. University of Toronto Press, Toronto, pp 637–659

Werdelin L, Turner A (1996b) Turnover in the guild of larger carnivores in Eurasia across the Miocene–Pliocene boundary. Acta Zool Crac 39: 585–592

Chapter 10. Inferences of social behavior in bone-cracking hyaenids (Carnivora, Hyaenidae) based on digital paleoneurological techniques: Implications for human–carnivoran interactions in the Pleistocene

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Summary: This work investigates the brain of three crania from two extinct species of *Crocuta* (*Crocuta spelaea* and *Crocuta ultima*) from the Late Pleistocene of Eurasia, by describing and comparing them with those of its extant relatives (especially *Crocuta crocuta*) to draw behavioral inferences and taxonomic conclusions.

Author's contribution: The doctoral candidate is the first author of this work. He was directly involved in all the stages of its development, incuding its original design, the CT processing and 3D modeling, the morphometric comparisons, and the writing of the manuscript.

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Inferences of social behavior in bone-cracking hyaenids (Carnivora, Hyaenidae) based on digital paleoneurological techniques: Implications for human–carnivoran interactions in the Pleistocene

Víctor Vinuesa [a], Dawid A. Iurino [b], Joan Madurell-Malapeira [a], [*], Jinyi Liu [c], Josep Fortuny [a], Raffaele Sardella [b], David M. Alba [a]

[a] Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, c/ de les columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain
[b] Dipartimento di Scienze della Terra, Sapienza Università di Roma, Piazzale Aldo Moro 5, 00185 Roma, Italy
[c] Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xi-Zhi-Men-Wai St, 10044 Beijing, China

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ABSTRACT

The putative competition between large predators and humans during the Pleistocene, especially in cave environments, has been a hotly debated topic during the last decades. Here, with the aid of digital paleoneurological techniques, we study the brain morphology and proportions of two fossil hyenas from the Eurasian Pleistocene, *Crocuta spelaea* and *Crocuta ultima*. Our results show that the brain morphology of these extinct species closely resembles that of the extant *Crocuta crocuta* and differs from those of the other extant genera (*Hyaena* and *Parahyaena*). Our analysis of brain proportions, however, shows a lesser development of the anterior brain in the extinct taxa compared with *C. crocuta*, thus more closely resembling the condition of both *Hyaena* and *Parahyaena*. The latter fact indicates that the greater anterior brain development of *C. crocuta* is a derived and recently-acquired trait, and suggests that extinct species of *Crocuta* displayed less-developed social abilities and/or a more restricted adaptability to new environments compared to the former. These behavioral differences between extinct and extant spotted hyenas might contribute to a better understanding of the taphonomical evidence obtained from Eurasian Pleistocene sites in relation to the ecological role played by humans and hyenas in the taphocenosis.

1. Introduction

The presence of large predators is considered one of the main factors that affected the successive human dispersal events across Eurasia during the Pleistocene (e.g., Turner, 1992; Turner and Antón, 1998; Rodríguez et al., 2012; Rodríguez-Gómez et al., 2013). Food acquisition must have been one of the key problems for these human populations to overcome, given the occurrence of periodic glaciations, so that several authors have suggested that the survival of Pleistocene hominins during the cold seasons was probably possible thanks to the scavenging of ungulate carcasses (Martínez-Navarro and Palmqvist, 1995; Arribas and Palmqvist, 1998; Palombo, 2014). The availability of these carcasses depends to a large extent on the internal structure of the carnivore guild and the intrinsic relationships between top predators (Rodríguez et al., 2012; Rodríguez-Gómez et al., 2013).

Based on available taphonomical evidence, it has been suggested that saber-toothed and conical-toothed cats, as well as bone-cracking hyenas, developed complex social pack-hunting behaviors (e.g., Palmqvist et al., 2011, and references therein). In the extinct hyaenids *Pachycrocuta brevirostris* and *Crocuta spelaea*, paleobiological inferences on social behavior have been made on the basis of bone accumulations from their putative dens (Boaz et al., 2000; Diedrich and Žák, 2006; Palmqvist et al., 2011). However, behavioral inferences on sociality can also be made within the framework of a research line initiated by Holekamp and coauthors (Holekamp et al., 2007a,b; Sakai et al., 2011), which has established a positive correlation between the relative size of the anterior brain and group size in hyaenids. According to the results of these

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[*] Corresponding author.
E-mail address: joan.madurell@icp.cat (J. Madurell-Malapeira).

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authors, among extant hyaenids the most social *Crocuta* would display the greatest development of the anterior brain, whereas the solitary *Proteles* would show the least. With the aid of computed tomography techniques (Iurino et al., 2013), this approach was recently applied to the late Pliocene to early Pleistocene European *Pliocrocuta perrieri* (see Vinuesa et al., 2015). Here, we follow the same approach to investigate the morphology and relative size of the internal cranial cavities in two fossil species of *Crocuta* (*Crocuta spelaea* from Europe and *Crocuta ultima* from Asia), and compare them with those of extant hyaenids in order make inferences on the social behavior in these extinct species.

2. Materials and methods

2.1. Studied and comparative sample

The studied specimens include two skulls of *C. spelaea* (MPD13 and MPD15) from Melpignano (Italy), housed in the Earth Sciences Department of the Sapienza University of Rome, and a skull of *C. ultima* (LXD007) from Lingxiandong cave (Qinhuangdao, Hebei province, China), housed in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science (Beijing, China). Melpignano has an estimated age of 100–70 ka (Bologna et al., 1994), whereas Lingxiandong cave has delivered a typical late middle to early late Pleistocene faunal assemblage (Liu et al., 2015).

The comparative sample includes CT-scans of extant bone-cracking hyenas, kindly provided by the Digimorph Team (www.digimorph.org): *Crocuta crocuta* (MVZ 184551, University of California Berkeley, Museum of Vertebrate Zoology, Berkeley, USA), *Parahyaena brunnea* (MVZ 117842, University of California Berkeley, Museum of Vertebrate Zoology, Berkeley, USA), and *Hyaena hyaena* (USNM 182034, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA).

2.2. CT-scanning parameters and endocast processing

Tomographic images of MPD15 and MPD13 (*C. spelaea*) were taken using a Philips Brilliance CT 64-channel scanner at M. G. Vannini Hospital (Rome), at 120 kV and 500 mA. The scanning resulted in 408 slices for MPD15 and 373 slices for MPD13. For both specimens, obtained pixel size is 0.39 mm, output image is 512 × 512 pixels per slice, and slices are 0.9 mm thick, with an interslice space of 0.45 mm. In turn, LXD007 was scanned at the Key Laboratory of Vertebrate Evolution and Human Origins using micro-computerized tomography developed by the Institute of High Energy Physics, Chinese Academy of Sciences (CAS), at 430 kV and 1.5 mA. A total of 2048 slices of 0.3 mm in width, with an interslice space of 0.2 mm, were obtained, resulting in an output image of 2048 × 2048 pixels per slice and a pixel size of 200 μm. The crania of extant taxa were scanned at the University of Texas High-Resolution Xray Computed Tomography Facility – Digital Morphology Group using the ACTIS CT scanner (for detailed scan parameters and further information, visit http://www.digimorph.org).

3D virtual models of the cranium and the endocranial cavities were derived from the CT-scans using Hounsfield units as reference units. Segmentation and 3D rendering of the specimens were computed using Avizo 7.0 (FEI-VSG, France). This software was also used to generate the 3D surfaces and volumes using the same steps for each CT-scan. Total and regional brain volumes were computed for all specimens with Rhinoceros 5.0 (McNeel, USA).

2.3. Regional brain volumes

In agreement with previous literature (Arsznov et al., 2010; Sakai et al., 2011; Swanson et al., 2012), virtual endocasts were subdivided into the following three regions, based on sulcal patterns and/or bony landmarks: anterior cerebrum, posterior cerebrum, and cerebellum plus brain stem (Fig. 1). To do so, endocasts were oriented so that the maximum length of the cerebrum plus the olfactory bulbs was situated along the horizontal plane. The anterior cerebrum was defined as the region situated caudally with respect to the olfactory bulbs and cranially with regard to the junction of the cruciate sulcus and the sagittal plane, whereas the posterior cerebrum was defined as the region situated caudally from the cruciate sulcus and extending to the cerebellum (more precisely, the tentorium; Sakai et al., 2011). The cerebellum plus brain stem region includes the volume of these two regions, placed at the posterior cranial fossa, which goes from the most anterior border of the tentorium to the foramen magnum (Sakai et al., 2011). Finally, the volume of the cerebrum corresponds to the sum of the anterior and posterior cerebrum volumes. Total and regional brain volumes for extant hyenas were taken from Sakai et al. (2011). To compute regional brain volumes in the fossil specimens, following Sakai et al. (2011) we relied on a ratio of the volume of each region relative to total brain cavity volume (which includes the olfactory bulbs, the cerebrum, the cerebellum, and the brain stem).

3. Results

3.1. Description of the internal cranial morphology

The specimen of *C. ultima* (LXD007; Fig. 2A–D) is generally well preserved, whereas the two specimens of *C. spelaea* are more partial: MPD13 lacks the brain stem (Fig. 2E–G), whereas MPD15 lacks the olfactory bulbs (Fig. 2H–J). However, all the major sulci and gyri can be observed in the virtual 3D models of the three specimens. In general terms, the three endocasts display a similar morphology, the most conspicuous difference between that of *C. ultima* and those of *C. spelaea* being the larger overall size of the former.

In the three studied specimens, the presylvian sulcus forms a dorsally-concave curve that, in lateral view, runs from the dorsal portion of the anterior cerebrum towards the frontobasal portion of the posterior cerebrum, reaching the sylvian sulcus below the coronal and suprasylvian sulci (Fig. 3A–C). Frontally and close to the longitudinal fissure, the three specimens display, more markedly in the right side, a small proreal sulcus that is parallel to the presylvian sulcus. This proreal sulcus runs towards the precruciate gyrus in *C. ultima*, but not in *C. spelaea*, in which it is less developed (Fig. 4A–C). In the three specimens, the sylvian sulcus displays a curved (dorsally-concave) contour, running from the frontobasal portion to the posterior region of the cerebrum. The ectosylvian sulcus is slightly curved and roughly parallel to the sylvian sulcus in

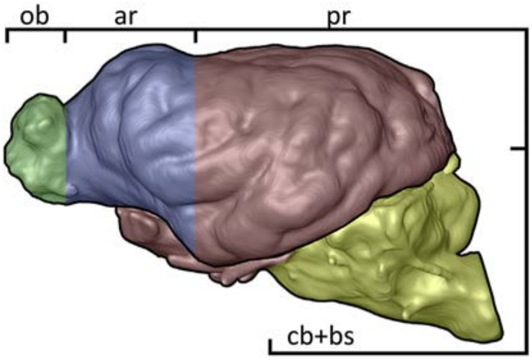

Fig. 1. Regional subdivisions of a hyaena brain according to Sakai et al. (2011). Abbreviations: ar, anterior region; cb + bs, cerebellum plus brain stem; ob, olfactory bulbs; pr, posterior region.

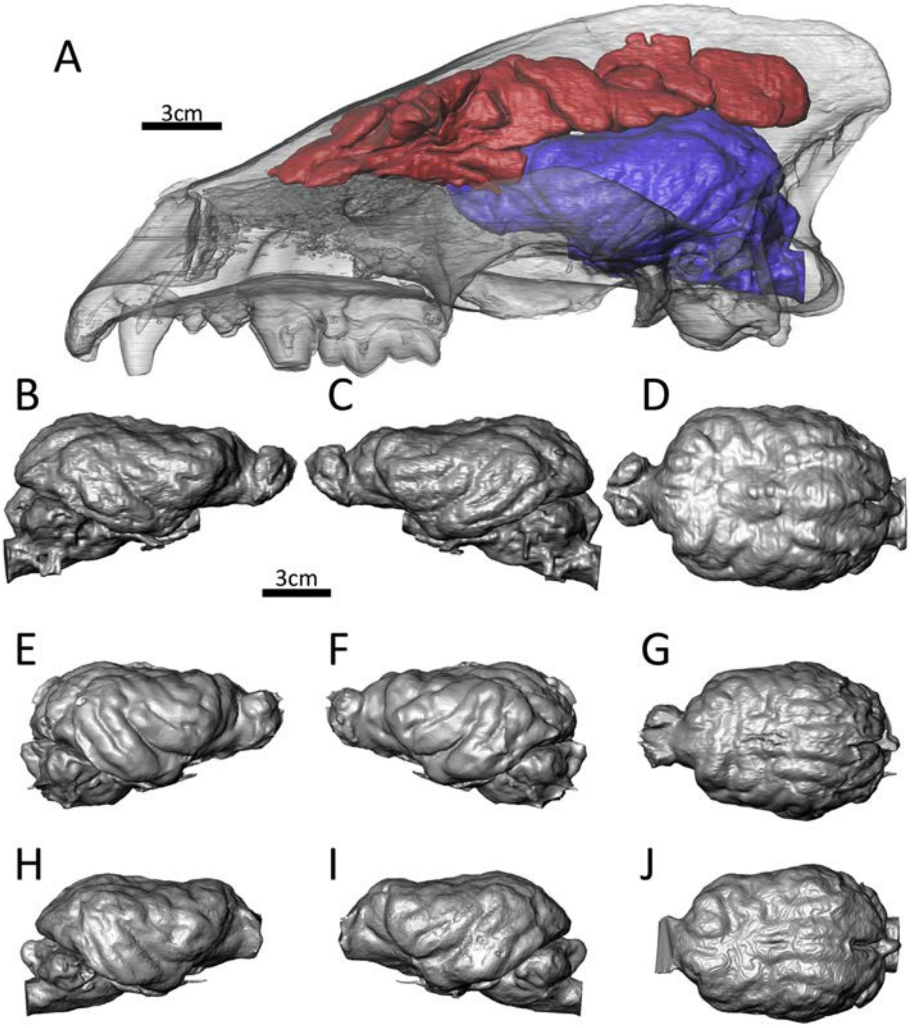

Fig. 2. Internal cranial morphology of *Crocuta ultima* and *Crocuta spelaea*. **A**, Cranium of *C. ultima* in left lateral view (translucent), showing the endocranial cavity (blue) and the frontal sinuses (red); **B–D**, Virtual endocast of *C. ultima* (LXD007) in (**B**), Right lateral; (**C**), Left lateral; (**D**), Dorsal view; **E–G**, Virtual endocast of *C. spelaea* (MPD13) in (**E**), Right lateral; (**F**), Left lateral; (**G**), Dorsal view; **H–J**, Virtual endocast of *C. spelaea* (MPD15) in (**H**), Right lateral; (**I**), Left lateral; (**J**), Dorsal view. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

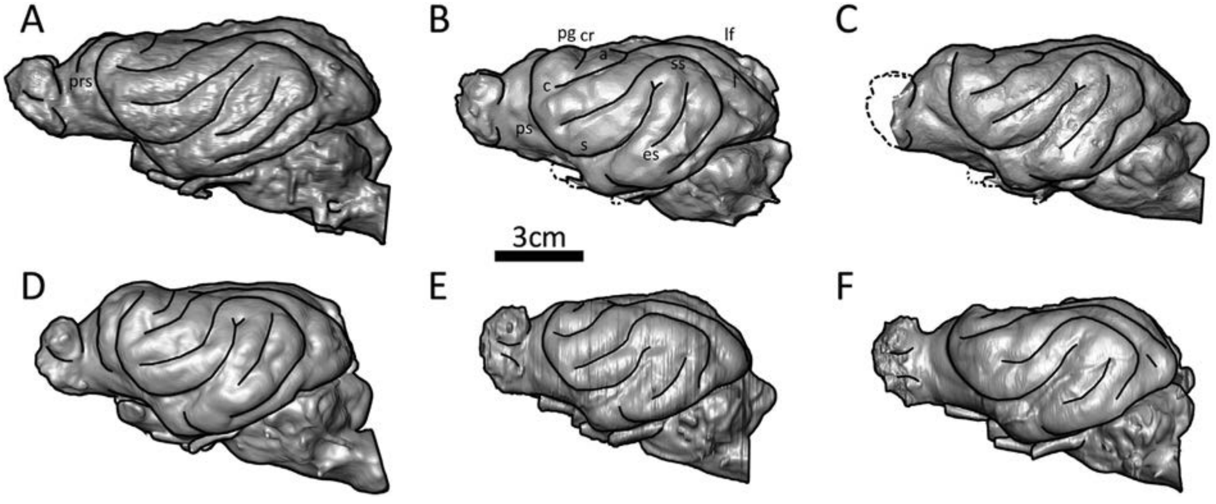

Fig. 3. Virtual endocasts in left lateral view of *Crocuta spelaea* and *Crocuta ultima* compared with those of extant bone-cracking hyaenids. **A**, *C. ultima* (LXD007); **B**, *C. spelaea* (MPD13); **C**, *C. spelaea* (MPD15); **D**, *Crocuta crocuta*; **E**, *Hyaena hyaena*; **F**, *Parahyaena brunnea*. Endocasts for extant taxa derived from data taken from Digimorph.org. Abbreviations: a, ansate sulcus; c, coronal sulcus; cr, cruciate sulcus; es, ectosylvian sulcus; l, lateral sulcus; lf, longitudinal fissure; pg, precruciate gyrus; prs, proreal sulcus; ps, presylvian sulcus; s, sylvian sulcus; ss, suprasylvian sulcus.

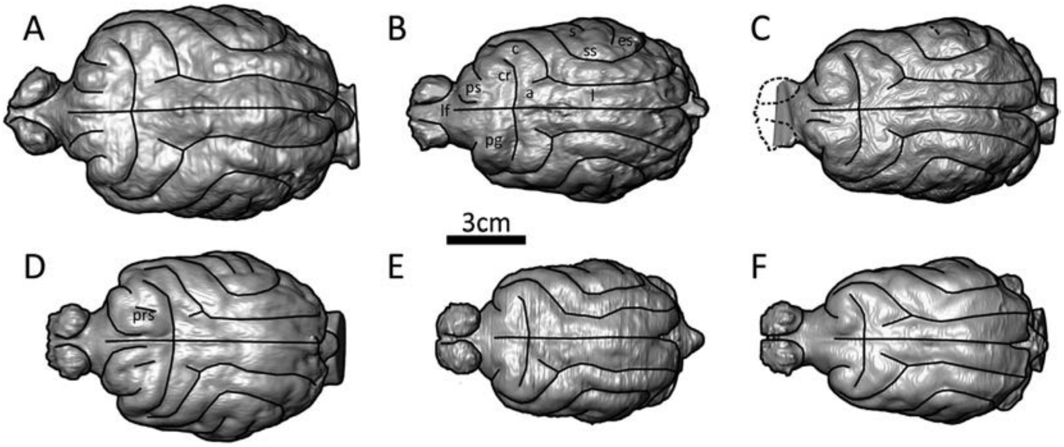

Fig. 4. Virtual endocasts in dorsal view of *Crocuta spelaea* and *Crocuta ultima* compared with those of extant bone-cracking hyaenids. **A**, *C. ultima* (LXD007); **B**, *C. spelaea* (MPD13); **C**, *C. spelaea* (MPD15); **D**, *Crocuta crocuta*; **E**, *Hyaena hyaena*; **F**, *Parahyaena brunnea*. Endocasts for extant taxa derived from data taken from Digimorph.org. Abbreviations as in Fig. 3.

the three studied fossil specimens (Fig. 3A–C). The suprasylvian sulcus originates in the anterior area, where it is parallel to the coronal and the sylvian sulci, becomes dorsally convex over the dorsal ends of the sylvian and ecotsylvian sulci, and ends with a curved caudal section parallel to the ectosylvian sulcus and to the cerebrum–cerebelum “limit”. The coronal sulcus runs parallel to and above the suprasylvian sulcus in all three studied specimens, with its frontal-most part being curved towards the dorsal area in *C. ultima* (Fig. 3A–C). The coronal sulcus posteriorly joins the lateral and the ansate sulci at a dorsal depression or “triple junction”, close to the longitudinal fissure (Fig. 4A–C). The lateral sulcus is roughly parallel to the longitudinal fissure from the posterior region of the cerebrum to its mid-area, in which the former ends at the “triple junction”. The ansate sulcus is partially preserved in the three specimens, starting at the dorsal depression or “triple junction”, in which the above-mentioned other sulci merge (Fig. 4A–C). The cruciate sulcus, which is anterior to the “triple junction” and posterior to the precruciate gyrus, is transversely long and well developed in all the three specimens, almost reaching the coronal sulcus in the external end, where it is slightly curved frontally (Fig. 4A–C).

3.2. *Brain morphology comparisons*

In general terms, the brain morphology and the sulcal pattern displayed by the three studied fossil endocasts is similar to that of the extant bone-cracking hyaenas (Figs. 3 and 4), which display more or less elongated olfactory bulbs, a variably expanded anterior cerebrum region (at the rostral cerebral fossa), and a trilobate cerebellum, There are, however, several differences compared to each of the three extant genera. The most obvious difference is related to the larger size and relatively more elongated brain of *C. ultima* compared with the extant taxa. Nevertheless, all the three studied endocasts clearly most closely resemble *C. crocuta* than either *Hyaena* or *Parahyaena* in the projection of the olfactory bulbs as well as in the overlap between the cerebrum and the cerebellum.

Regarding sulcal morphology, there are also several differences between the studied fossil specimens and extant bone-cracking hyenas, especially when compared to either *Hyaena* or *Parahyaena*. It is noteworthy the presence of a proreal sulcus anterior to the presylvian sulcus in the three studied specimens (albeit variously developed), since this feature is displayed by *C. crocuta* but not *Hyaena* or *Parahyaena* (Fig. 4). The curvature of the presylvian sulcus is most similar between *C. crocuta* and *C. ultima*, displaying a less pronounced curvature in the two specimens of *C. spelaea* (particularly MPD15). In the three fossil specimens, the sylvian sulcus is longer than in *Hyaena* and *Parahyaena*, since it extends more dorsally and closer to the suprasylvian sulcus. In this regard, both *C. ultima* and *C. spelaea* more closely resemble the condition of the extant *C. crocuta*, although *C. crocuta* and *C. spelaea* displays a terminal fork not observed in *C. ultima* (Fig. 3A–D). The coronal sulcus is quite straight in the two specimens of *C. spelaea*, thus resembling the condition of *C. crocuta*, whereas in *C. ultima* it displays a small dorsal curvature in its anterior end (as in *Hyaena*, but unlike in *Parahyaena*). On the other hand, in the three studied specimens the coronal sulcus is longer than in *C. crocuta* and *Hyaena*, in which it is rather short, thus most closely resembling the condition seen in *Parahyaena* (Fig. 4). The morphology of the suprasylvian sulcus in the fossil endocasts generally resembles the condition displayed by *C. crocuta*. However, the anterior portion of the suprasylvian sulcus is straight in the two specimens of *C. spelaea*, as in *Hyaena*, whereas in *C. ultima* it is slightly curved towards the dorsal area, as in *C. crocuta* (thus not reaching the more marked curvature displayed by *Parahyaena*; Fig. 3). In the studied fossil specimens, the medial-dorsal area of the suprasylvian sulcus is narrow, especially when compared with *Hyaena* and *Parahyaena*, although it is less dorsally projected or rotated towards the dorsal area than in *C. crocuta*. The posterobasal end of the suprasylvian sulcus is quite long in the three fossil endocasts, in which it runs parallel to the brain-cerebellum limit (as in *C. crocuta*, but unlike in *Hyaena* and *Parahyaena*; Fig. 3). Finally, the cruciate sulcus displays a similar length and morphology in the studied specimens and in the three extant species, although its relative position within the brain varies to some extent. Thus, in the fossil specimens the cruciate sulcus is more anteriorly located than in the extant *C. crocuta*, thus more closely resembling the condition observed in *Hyaena* and in *Parahyaena*.

3.3. *Relative regional volumes*

Total brain volume of the studied specimens is reported in Table 1 and Fig. 5. The largest specimen is that of *C. ultima* (LDX007), with an estimated brain volume of 278 cm^3, followed by those of *C. spelaea* (218 cm^3 in MPD13 and 174 cm^3 in MPD15). Although these specimens are somewhat larger than the average value for *C. crocuta* (160 cm^3), they more closely resemble the latter taxon than the two remaining extant bone-cracking hyenas, which display considerably lower total brain volumes on average (104 cm^3 in *Hyaena* and 111 cm^3 in *Parahyaena*). Although the difference between the two specimens of *C. spelaea* might seem caused by the

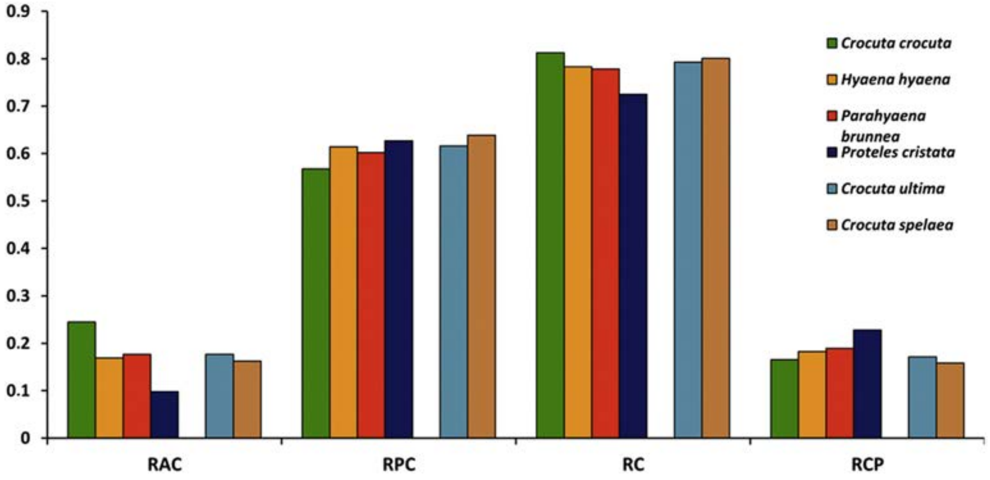

Fig. 5. Histograms of relative regional brain volumes in *Crocuta spelaea* and *Crocuta ultima*, compared with those of extant hyaenids. See Table 1 for numerical results. Abbreviations: RAC, relative anterior cerebrum volume; RC, relative cerebrum volume; RCP, relative cerebellum plus brain stem volume; RPC, relative posterior cerebrum volume. Data for extant taxa taken from Sakai et al. (2011).

lack of the olfactory bulbs (which usually takes only around 4–5% of total brain volume) in MPD15, this difference does not imply a bias in the obtained regional volumes.

Table 1
Total and regional endocranial volumes in *Crocuta spelaea* and *Crocuta ultima*, compared to mean species values for extant hyaenids.

Species	ECV	ACV	PCV	CV	CSV	RAC	RPC	RC	RCP
Crocuta crocuta	160,058.94	39,181.02	90,882.65	130,063.67	26,474.06	0.245	0.568	0.813	0.165
Parahyaena brunnea	111,010.33	19,624.81	66,813.21	86,438.02	21,025.3	0.177	0.602	0.779	0.189
Hyaena hyaena	104,114.17	17,601.17	63,953.03	81,554.2	19,004.23	0.169	0.614	0.783	0.183
Proteles cristatus	38,105.87	3,742.81	23,887.75	27,630.56	8702.96	0.098	0.627	0.725	0.228
Crocuta spelaea (MPD13)	218,383.27	36,201.07	139,525.17	175,726.24	33,583.99	0.166	0.639	0.805	0.154
Crocuta spelaea (MPD15)	174,205.31	28,170.30	113,136.82	141,307.12	28,828.62	0.159	0.638	0.797	0.162
Crocuta ultima (LXD007)	278,160.87	49,121.22	171,390.58	220,511.80	47,687.38	0.177	0.616	0.793	0.171

Abbreviations: ACV, anterior cerebrum volume (in mm^3); CSV, cerebellum plus brain stem volume (in mm^3); CV, total cerebrum volume (in mm^3) ECV, total endocranial volume (in mm^3); PCV, posterior cerebrum volume (in mm^3); RAC, relative anterior cerebrum volume (computed as ACV/ECV); RCP, relative cerebellum plus brain stem volume (computed as CSV/ECV); RC, relative cerebrum volume (computed as CV/ECV); RPC, relative posterior cerebrum volume (computed as PCV/ECV). Data for extant taxa taken from Sakai et al. (2011).

Crocuta ultima displays the largest anterior cerebrum volume (49 cm^3), representing 17.7% of total brain volume. *Crocuta spelaea*, in turn, has an anterior volume of 36 cm^3 in MPD13 and of 28 cm^3 in MPD15, respectively representing 16.6% and 15.9% of total brain volume. These figures of relative volume of the anterior cerebrum are thus similar among the two extinct species, but far below the average values displayed by extant *C. crocuta*, in which the anterior cerebrum represents a greater portion of the whole brain (39 cm^3, 24.5%). The values of 16–18% displayed by the extinct species of *Crocuta* more closely resemble the average values of the two other extant bone-cracking hyenas (16.9% in *Hyaena* and 17.7% in *Parahyaena*), while being higher than in the extant *Proteles* (10%; Fig. 5). In turn, the size of the posterior cerebrum region relative to total endocranial volume in *C. spelaea* (64% in the two specimens) and in *C. ultima* (62%) is higher than the average of *C. crocuta* (57%) and, to a lesser extent, than the mean values of *Hyaena* (60%) and *Parahyaena* (61%), more closely resembling the condition of *Proteles* (63%).

4. Discussion

4.1. Phylogenetic implications of brain morphology

External (dental and postcranial) differences between Pleistocene spotted hyenas throughout Africa and Eurasia are relatively minor and mostly relate to overall size and the degree of shortening of the distal limb elements (radius and tibia; Turner and Antón, 1996; Palmqvist et al., 2011). Given these relatively restricted differences, during the last decades there has been a debate about the taxonomic status and phylogenetic position of Eurasian spotted hyenas (see Werdelin and Solounias, 1991), which are customarily assigned to *C. spelaea* in the case of Europe and to *C. ultima* in the case of its Asian counterpart (Baryshnikov, 2014). In the past, fossil spotted hyenas were merely distinguished as subspecies of the extant *Crocuta crocuta* by some authors, e.g., *Crocuta crocuta spelaea* (Kurtén, 1957; Werdelin and Solounias, 1991), *Crocuta crocuta praespelaea* (Schütt, 1971), or *Crocuta crocuta ultima* (Kurtén, 1956; Liu, 1999; Tseng and Chang, 2007). Alternatively, some authors have assigned these taxa to the extant species *C. crocuta* without distinguishing subspecies (Werdelin and Solounias, 1991; Sardella and Petrucci, 2012). It is beyond the scope of this paper to refute or further justify any of these taxonomic schemes, since this would require examining other features relating to external cranial morphology as well as postcranial and dental proportions. However, as discussed below, the data reported here shed new light on the evolutionary history of the *Crocuta* lineage from a paleoneurological viewpoint.

The study of ancient and recent DNA has confirmed the existence of gene flow between the African and Eurasian populations of spotted hyenas throughout the Pleistocene (Rohland et al., 2005; Sheng et al., 2014), further suggesting that several dispersal events took place during the Middle and Late Pleistocene. Rohland et al. (2005) suggested that the genus *Crocuta* originated in Central Africa ca. 3.5 Ma and subsequently performed three successive dispersal events ('migration waves') out of Africa: into Eastern Eurasia (<3.5 Ma); into Europe and South Africa (1.5–1.3 Ma); and finally into all of Eurasia (<130 ka). However, Rohland et al. (2005) did not provide specific data on the origin of the extant species *C. crocuta*. More recently, Sheng et al. (2014) similarly proposed an African origin for the genus *Crocuta*, but suggested instead the existence of two migration waves from Eurasia into Africa at 430 ka and 63 ka. These authors further suggested a Eurasian origin for the extant African species *C. crocuta*, which would have originated from an ancestral Eurasian population that retreated into Africa. According to Sheng et al. (2014), accurately dating the appearance of modern *C. crocuta* is hindered by the scarce Late Pleistocene record of spotted hyaenas outside China and Europe.

Based on the studied fossil endocasts, there are no remarkable differences between the two extinct studied species, *C. ultima* and *C. spelaea*, except for the somewhat larger brain size of the former. Their overall brain morphology is more similar to that of *C. crocuta* than to that of the other extant bone-cracking hyenas, as it might be expected with their closer taxonomic affinities with the former. Similarities include the presence of a proreal sulcus located close to the presylvian sulcus and the length and curvature of the major sulci (e.g., the development and length of the suprasylvian sulcus). However, the two studied extinct species similarly differ from extant *C. crocuta* (and more closely resemble the two other extant bone-cracking hyenas, *Parahyaena* and *Hyaena*) in several features, particularly the position of the cruciate sulcus and the relative size of the anterior cerebrum. This suggests that, in some regards, the studied Eurasian specimens of *Crocuta* are more primitive than extant *C. crocuta* from Africa, which would autapomorphically differ by its greater development of the frontal portion of the brain.

Based on the current fossil record and the above-mentioned molecular analyses, the most likely evolutionary scenario for the genus *Crocuta* includes an African origin, being already recorded in this continent by *Crocuta dietrechi* at 3.85–3.63 Ma (Turner, 1990; Werdelin and Lewis, 2005; Deino, 2011). Subsequently, this genus would have first dispersed into Asia by the earliest Pleistocene (ca. 2.2 Ma; Qiu et al., 2004) and into Europe around the early-middle Pleistocene (ca. 0.8 Ma; García and Arsuaga, 2001; Sardella and Petrucci, 2012). The results reported in this paper for Pleistocene Eurasian *Crocuta* suggest that the greater development of the anterior brain in extant *C. crocuta* from Africa is a recent evolutionary acquisition, probably postdating the last inferred dispersal event from Eurasia into Africa at ca. 63 ka (Sheng et al., 2014). This would explain the retention of a relatively smaller anterior cerebrum and other primitive brain features, not only in *C. ultima* (late middle to early late Pleistocene), by also in *C. spelaea* (100–70 ka). Additional specimens from both Eurasia and Africa and with different ages would be required to further confirm the time of appearance of this particular character within the genus *Crocuta*.

4.2. Behavioral implications

Besides its hunting ability, the genus *Crocuta* differs from the other extant bone-cracking hyaenas by its highly-developed sociability (Kruuk, 1972; Mills, 1990; Cooper et al., 1999). Thus, highly complex social behaviors have been documented in the living *C. crocuta*, being even considered comparable to those displayed by some cercopithecid monkeys (Holekamp et al., 2015, and references therein). This is more difficult to ascertain in the case of fossil hyaenids, although some inferences have been drawn on the basis of taphonomical studies of bone accumulations (e.g., Turner and Antón, 1996; Boaz et al., 2000; Palmqvist et al., 2011), showing the principal role of *C. spelaea* or *Pachycrocuta brevirostris* as bone accumulators. Moreover, Palmqvist et al. (2011) analyzed the scavenging abilities of Pleistocene spotted hyenas and concluded that some features displayed by both *C. spelaea* and *P. brevirostris* (i.e., shortening of distal limb segments) might have been convergently acquired by these taxa as an adaptation to scavenging habits.

Behavioral inferences in extinct hyaenids can be further complemented by paleoneurological studies. In particular, a series of recent papers by Holekamp and coauthors (Holekamp et al., 2007a,b, 2015; Arsznov et al., 2010; Sakai et al., 2011) have shown that regional brain proportions (and, in particular, the development of the frontal area of the brain, where the frontal cortex is situated) are correlated with social behavior among extant hyaenids, with the most social *C. crocuta* displaying the greatest development of this region. Besides including several other anatomical structures, the anterior region of the brain is mainly constituted by the frontal cortex, which in primates and other mammals intervenes in complex cognitive processes related to social decision-making, including the inhibitory behaviors that are required in complex fission–fusion societies. Therefore, a relatively larger frontal cortex is considered to reflect enhanced abilities regarding the processing of social information (Adolphs, 2001; Amodio and Frith, 2006; Sakai et al., 2011). This is supported by a recent study of the correlation between total and regional brain volumes with several behavioral variables in carnivorans as a whole, which concluded that, although there is no support for a role of social complexity in overall encephalization, relative regional brain volumes are correlated with other variables, such as foraging habits and home range (Swanson et al., 2012). These authors further concluded that the relationship between the development of the anterior brain and sociability cannot be extended to carnivorans as a whole, thereby suggesting that each family should be studied separately.

Although sociability is the most plausible explanation for the enlargement of the anterior brain in *Crocuta*, Holekamp et al. (2015) suggested that other factors, such as diet or the behavioral flexibility (the "cognitive buffer" hypothesis, see below; Reader and MacDonald, 2003; Richardson and Boyd, 2000; Sol, 2009a,b; Holekamp et al., 2015), might be involved. The link between AC volumen and diet is based on the fact that the species with a more developed anterior brain (*C. crocuta*) eats mainly antelopes and other fresh meat, whereas the species with a moderately-developed brain (*H. hyaena* and *P. brunnea*) eat mainly carrion, and the species with a less developed anterior region (*Proteles cristata*) is an insectivore. In turn, according to the "cognitive buffer" hypothesis, large brains would help animals to deal with new and unpredictable environments, by enabling individuals to exhibit a more flexible behavior. This fits well with extant hyaenids, as *C. crocuta* is the species that most commonly experience such varying environmental conditions and displays greater flexibility in foraging habits and other social behaviors. In this regard, different environmental conditions across the past distribution range of *Crocuta* might have also impacted on the evolution of their sociality, in particular by favoring the acquisition of more complex social behaviors in those species or populations inhabiting open habitats, as recently pointed by Smith et al. (2012). By taking all these considerations into account, the lesser anterior brain volume displayed by *C. spelaea* and *C. ultima* compared to extant *C. crocuta* (i.e., more comparable to those of *Hyaena* and *Parahyaena*, in spite of a more distant phylogenetic relationship) may be interpreted as indicating reduced social abilities, dietary differences and/or a lesser behavioral flexibility when faced to new or unpredictable environments.

The relative development of the anterior area of the brain and their correlation with social behavior was recently investigated in the Villafranchian bone-cracker *Pliocrocuta perrieri* (Vinuesa et al., 2015). These authors showed that this extinct hyaenid displays a brain morphology more similar to that of *Hyaena* and *Parahyaena* as well as a relatively small anterior brain portion similar to these taxa and smaller than in the extant *Crocuta*. On this basis, Vinuesa et al. (2015) concluded that *P. perrieri* probably displayed less developed social abilities than *C. crocuta*. Similarly, the smaller anterior brain of *C. spelaea* and *C. ultima* compared with extant *C. crocuta* (and, thus, more comparable to that of *Hyaena* and *Parahyaena*) would also imply that these fossil species of *Crocuta* from Eurasia possessed less developed social abilities, presumably resulting in a lower adaptability to new and unpredictable environments than in extant spotted hyenas.

The results reported here are relevant regarding the putative competition between fossil Eurasian spotted hyaenas and extinct species of *Homo* such as Neandertals (e.g., Caparrós et al., 2012; Patou-Mathis, 2012; Rosell et al., 2012; Dusseldorp, 2013), which has been hotly debated, especially in the framework of cave environments (Diedrich and Žák, 2006; Rosell et al., 2012). The bone accumulations generated by fossil spotted hyenas in caves have been compared with present-day examples of hyena dens in eastern and southern Africa (Diedrich and Žák, 2006; Dusseldorp, 2013). However, our results suggest that the social and/or foraging behavior of extinct species of *Crocuta* might have been quite different from those of their extant counterparts, and that, consequently, other extant bone-cracking hyenas might be in some regards better analogues to be used in taphonomical studies.

5. Conclusions

Based on virtual endocasts, here we describe the morphology and analyze the relative proportions of the brain in two extinct species of spotted hyena from Eurasia, *C. spelaea* and *C. ultima*, in order to make phylogenetic and behavioral inferences. Our results show that their brain morphology is generally more similar to that of the extant *C. crocuta* than to that of the other extant bone-cracking hyenas (*Hyaena* and *Parahyaena*). However, the anterior brain volume of these extinct hyeanas more closely resembles that of *Hyaena* and *Parahyaena* than the extant *C. crocuta*, which displays the largest relative size of this region among extant hyaenids. Our results suggest that the greater development of the frontal region of the brain is a relatively recent acquisition in the *Crocuta* lineage, being probably related to enhanced foraging behaviors (such as pack-hunting) and/or other complex behaviors. The presumably less developed social abilities of extinct *Crocuta* (probably more similar to other exant bone-cracking hyenas) should be taken into account when interpreting the bone accumulations generated by these species and, in the future, it may shed light on studies about the competition between hyaenas and humans during the Pleistocene.

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References

Adolphs, R., 2001. The neurobiology of social cognition. Current Opinion in Neurobiology 11, 231–239.

Amodio, D.M., Frith, C.D., 2006. Meeting of minds: the medial frontal cortex and social cognition. Nature Reviews Neuroscience 7, 268–277.

Arribas, A., Palmqvist, P., 1998. Taphonomy and palaeoecology of an assemblage of large mammals: hyaenid activity in the Lower Pleistocene site at Venta Micena (Orce, Guadix-Baza Basin, Granada, Spain). Geobios 31 (S3), 3–47.

Arsznov, B.M., Lundrigan, B.L., Holekamp, K.E., Sakai, S.T., 2010. Sex and the frontal cortex: a developmental CT study in the spotted hyena. Brain Behavior and Evolution 76, 185–197.

Baryshnikov, C.F., 2014. Late Pleistocene hyena *Crocuta ultima ussurica* (Mammalia: Carnivora: Hyaenidae) from the Paleolithic site in geographical society cave in the Russian far east. Proceedings of the Zoological Institute RAS 318, 197–225.

Boaz, N.T., Ciochon, R.L., Xu, Q., Liu, J., 2000. Large mammalian carnivores as a taphonomic factor in the bone accumulation at Zhoukoudian. Acta Anthropologica Sinica 19, 224–234.

Bologna, P., Di Stefano, G., Manzi, G., Petronio, C., Sardella, R., Squazzini, E., 1994. Late Pleistocene mammals from the Melpignano (LE) "Ventarole": preliminary analysis and correlations. Bollettino della Società Paleontologica Italiana 33, 265–274.

Caparrós, M., Ruiz, C.B., Moigne, A.M., Bohórquez, A.M., 2012. Did Neanderthals and carnivores compete for animal nutritional resources in the surroundings of the Cave of Zafarraya? Journal of Taphonomy 10, 395–415.

Cooper, S.M., Holekamp, K.E., Smale, L., 1999. A seasonal feast: long term analysis of feeding behaviour in the spotted hyaena (*Crocuta crocuta*). African Journal of Ecology 37, 149–160.

Deino, A., 2011. 40Ar/39Ar dating of Laetoli, Tanzania. In: Harrison, T. (Ed.), Paleontology and Geology of Laetoli: Human Evolution in Context, Geology, Geochronology, Paleoecology and Paleoenvironment, vol. 1. Springer, New York, pp. 77–97.

Diedrich, C., Žák, K., 2006. Prey deposits and den sites of the Upper Pleistocene hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) in horizontal and vertical caves of the Bohemian Karst (Czech Republic). Bulletin of Geosciences 81, 237–276.

Dusseldorp, G.L., 2013. Neanderthals and cave hyenas: Co-existence, competition or conflict? In: Clark, J.L., Speth, J.D. (Eds.), Zooarchaeology and Modern Human Origins. Springer, Dordrecht, pp. 191–208.

García, N., Arsuaga, J.L., 2001. Les carnivores (Mammalia) des sites du Pleistocène ancient et moyen d'Atapuerca (Espagne). L'Anthropologie 105, 83–93.

Holekamp, K.E., Sakai, S.T., Lundrigan, B.L., 2007a. Social intelligence in the spotted hyena (*Crocuta crocuta*). Philosophical Transactions of the Royal Society of London B 362, 523–538.

Holekamp, K.E., Sakai, S.T., Lundrigan, B.L., 2007b. The spotted hyena (*Crocuta crocuta*) as a model system for study of the evolution of intelligence. Journal of Mammalogy 88, 545–554.

Holekamp, K.E., Dantzer, B., Stricker, G., Yoshida, K.C.S., Benson-Amram, S., 2015. Brains, brawn and sociality: a hyaena's tale. Animal Behaviour 103, 237–248.

Iurino, D.A., Danti, M., Della Sala, S.W., Sardella, R., 2013. Modern techniques for ancient bones: vertebrate palaeontology and medical CT analysis. Bollettino della Società Paleontologica Italiana 52, 145–155.

Kruuk, H., 1972. The Spotted Hyena: Study of Predation and Social Behavior. Chicago University Press, Chicago.

Kurtén, B., 1956. The status and affinities of *Hyaena sinensis* Owen and *Hyaena ultima* Matsumoto. American Museum Novitates 1764, 1–48.

Kurtén, B., 1957. The bears and hyaenas of the interglacials. Quaternaria 4, 69–81.

Liu, J., 1999. Late Pleistocene mammal fossils from Miaofengshan, Beijing and discussion of *Crocuta crocuta ultima*. Longgupo Prehistoric Culture 1, 128–139 in Chinese with English summary.

Liu, J., Wagner, J., Chen, P., 2015. Mass mortality of a large population of the spotted hyenas (*Crocuta ultima*) at the Lingxiandong Cave, Qinhuangdao, Hebei Province: a hyena communal den with its palaeoecological and taphonomic interpretation. Quaternary Science 35, 607–621 in Chinese with English summary.

Martínez-Navarro, B., Palmqvist, P., 1995. Presence of the African machairodont *Megantereon whitei* (Broom 1937) (Felidae, Carnivora, Mammalia) in the Lower Pleistocene site of Venta Micena (Orce, Granada, Spain), with some considerations on the origin, evolution and dispersal of the genus. Journal of Archaeological Science 22, 569–582.

Mills, G., 1990. Kalahari Hyaenas. The Comparative Behavioural Ecology of Two Species. Unwin Hyman, London.

Palmqvist, P., Martínez-Navarro, B., Pérez-Claros, J.A., Torregrosa, V., Figueirido, B., Jiménez-Arenas, J.M., Espigares, M.P., Ros-Montoya, S., De Renzi, M., 2011. The giant hyena *Pachycrocuta brevirostris*: modelling the bone-cracking behavior of an extinct carnivore. Quaternary International 243, 61–79.

Palombo, M.R., 2014. Deconstructing mammal dispersals and faunal dynamics in SW Europe during the quaternary. Quaternary Science Reviews 96, 50–71.

Patou-Mathis, M., 2012. Interactions between Neanderthals and carnivores in Eastern Europe. Journal of Taphonomy 10, 277–290.

Qiu, Z., Deng, T., Wang, B., 2004. Early Pleistocene mammalian faunas from Longdan, Congxiang, Gansu, China. Palaeontologia Sinica 191, 1–198.

Reader, S.M., MacDonald, K., 2003. Environmental variability and primate behavioural flexibility. In: Reader, S.M., Laland, K.N. (Eds.), Animal Innovation. Oxford University Press, Oxford, U.K, pp. 83–116.

Richardson, P.J., Boyd, R., 2000. Climate, culture and the evolution of cognition. In: Heyes, C., Huber, L. (Eds.), The Evolution of Cognition. MIT Press, Cambridge, MA, pp. 329–346.

Rodríguez, J., Rodríguez-Gómez, G., Martín-González, J.A., Goikoetxea, I., Mateos, A., 2012. Predator–prey relationships and the role of *Homo* in Early Pleistocene food webs in Southern Europe. Palaeogeography Palaeoclimatology and Palaeoecology 365, 99–114.

Rodríguez-Gómez, G., Rodríguez, J., Martín-González, J.Á., Goikoetxea, I., Mateos, A., 2013. Modeling trophic resource availability for the first human settlers of Europe: the case of Atapuerca TD6. Journal of Human Evolution 64, 645–657.

Rohland, N., Pollack, J.L., Nagel, D., Beauval, C., Airvaux, J., Pääbo, S., Hofreiter, M., 2005. The population history of extant and extinct hyenas. Molecular Biology and Evolution 22, 2435–2443.

Rosell, J., Baquedano, E., Blasco, R., Camarós, E., 2012. New insights on hominid-carnivore interactions during the Pleistocene. Journal of Taphonomy 10, 125–128.

Sakai, S.T., Arsznov, B.M., Lundrigan, B.L., Holekamp, K.E., 2011. Brain size and social complexity: a computed tomography study in Hyaenidae. Brain Behavior and Evolution 77, 91–104.

Sardella, R., Petrucci, M., 2012. The earliest middle Pleistocene *Crocuta crocuta* (Erxlebenm 1777) at Casal Selce (Rome, Italy). Quaternary International 267, 103–110.

Schütt, G., 1971. Die Hyänen der Mosbacher Sande (Altpleistozän, Wiesbaden/Hessen) mit einem Beitrag zur Stammesgeschichte der Gattung *Crocuta*. Mainzer naturwissenschaftliches Archiv 10, 29–76.

Sheng, G.L., Soubrier, J., Liu, J.Y., Werdelin, L., Bastien, L., Thomson, V.A., Tuke, J., Wu, L.J., Hou, X.D., Chen, Q.J., 2014. Pleistocene Chinese cave hyenas and the recent Eurasian history of the spotted hyena, *Crocuta crocuta*. Molecular Ecology 23, 522–533.

Smith, J.E., Swanson, E.M., Reed, D., Holekamp, K.E., 2012. Evolution of cooperation among mammalian carnivores and its relevance to hominin evolution. Current Anthropology 53, S436–S452.

Sol, D., 2009a. The cognitive-buffer hypothesis for the evolution of large brains. In: Dukas, R., Ratcliffe, R.M. (Eds.), Cognitive Ecology II. Chicago University Press, Chicago, IL, pp. 111–136.

Sol, D., 2009b. Revisiting the cognitive buffer hypothesis for the evolution of large brains. Biology Letters 5, 130–133.

Swanson, E.M., Holekamp, K.E., Lundrigan, B.L., Arsznov, B.M., Sakai, S.T., 2012. Multiple determinants of whole and regional brain volume among terrestrial carnivorans. PLoS ONE 7, e38447.

Tseng, Z.J., Chang, C., 2007. A study of new material of *Crocuta crocuta ultima* (Carnivora: Hyaenidae) from the quaternary of Taiwan. Collection and Research 20, 9–19.

Turner, A., 1990. The evolution of the guild of larger terrestrial carnivores during the Plio-Pleistocene in Africa. Geobios 23, 349–368.

Turner, A., 1992. Large carnivores and earliest European hominids: changing determinants of resource availability during the lower and middle Pleistocene. Journal of Human Evolution 22, 109–126.

Turner, A., Antón, M., 1996. The giant hyaena *Pachycrocuta brevirostris* (Mammalia, Carnivora, Hyaenidae). Geobios 29, 455–468.

Turner, A., Antón, M., 1998. Climate and evolution: implications of some extinction patterns in African and European machairodontine cats of the Plio-Pleistocene. Estudios Geológicos 54, 209–230.

Vinuesa, V., Madurell-Malapeira, J., Fortuny, J., Alba, D.M., 2015. The endocranial morphology of the Plio-Pleistocene bone-cracking hyena *Pliocrocuta perrieri*: behavioral implications. Journal of Mammalian Evolution 22, 421–434.

Werdelin, L., Lewis, M.E., 2005. Plio-Pleistocene Carnivora of eastern Africa: species richness and turnover patterns. Zoological Journal of the Linnean Society 144, 121–144.

Werdelin, L., Solounias, N., 1991. The Hyaenidae: taxonomy, systematics and evolution. Fossils and Strata 30, 1–104.

Chapter 11. Discussion

This chapter recapitulates and contextualizes the most relevant results of chapters 4–10, and discusses them by pivoting around four main topics: new contributions to the paleobiology and evolution of bone-cracking hyenas; the evolution of durophagy; paleoneurology; and an updated overview of hyaenid phylogeny.

11.1. New contributions to the paleobiology and evolution of bone-cracking hyenas

The papers that constitute the core of this dissertation (reproduced in the various chapters of the Results) include multiple contributions to various aspects related to the paleobiology and evolution of bone-cracking hyenas, namely taxonomy, systematics and dietary adaptations. The most important contributions for each of the investigated genera are summarized and further discussed below.

11.1.1. *Hyaenictis*

Chapter 4 describes a previous unpublished hyaenid skull from Ronda Oest de Sabadell, which is attributed to *Hyaenictis* aff. *almerai*. This represents a significant improvent to the knowledge of this genus in Europe, where it was previously represented by just two hemimandibles ascribed to two different species (Werdelin and Solounias, 1991; Turner et al., 2008): *Hyaenictis graeca* from Pikermi (MN10, Greece) and *Hyaenictis almerai* from Sant Miquel de Toudell in Viladecavalls (MN10, Spain). The only *Hyaenictis* remains outside Europe belong to *Hyaenictis hendeyi* (Pliocene, ca. 5 Ma, South Africa; Werdelin et al., 1994) and some isolated teeth of attributed to this genus from a few other African sites (e.g., Werdelin and Peigné, 2010). The studied specimen represents the most completely known specimen of *Hyaenictis* and the most relevant contribution to the knowledge of this genus since Werdelin and Turner (1994) erected *Hyaenictis hendeyi*. The attribution of the described material to *Hyaenictis* is based on a mixture of primitive and derived characters that is characteristic of this genus. The new material does not fit well with any of the previously known species, from which it differs by more durophagous features (e.g., broader premolars, as in *Adcrocuta*). The tentative attribution of this material to *Hyaenictis* aff. *almerai* (using open nomenclature) is justified by the closer morphologic similarities with the material from Sant Miquel de Toudell, together with the geographical and chronological proximity (same MN and basin). From a paleobiological viewpoint, the morphometric analyses of cheek tooth proportions support the possession of durophagous adaptations in the described specimen, which differs by its buccolingually broader cheek teeth from all of the other known species of the genus. These analyses place the described specimen between other known species of ecomorphotype 4 (cursorial meat-eaters) and *Adcrocuta* (the first fully developed bone-cracker of the ecomorphotype 6). This morphological proximity to *Adcrocuta*, added to the presence of a zig-zag pattern on the enamel microstructure and the other craniodental durophagous traits described, supports the view that this specimen was close to be a fully developed bone-cracker from ecomorphotype 6, thereby likely belonging to ecomorphotype 5 (transitional bone-cracking hyenas). According to this, *Hyaenictis* aff. *almerai* would be the first member of the *Chasmaporthetes* clade to be included in this ecomorphotype since Werdelin and Solounias (1996) described the hunting hyenas ecomorphotype 4, thus contradicting the hypothesis that all the species belonging to the *Chasmaporthetes* clade would have been adapted towards hypercarnivorism (Werdelin and Turner, 1994).

11.1.2. *Pliocrocuta*

Two chapters of this dissertation are focused on the genus *Pliocrocuta*. Chapter 5 provides a description of the external morphology of three previously unpublished crania from the Late Pliocene of Villarroya (Spain) and the Early Pleistocene of La Puebla de Valverde (Spain), as well as comparisons with other published remains of *Pliocrocuta perrieri* from the Old World and two Eurasian hyaenids from the Pliocene and Early Pleistocene (*Chasmaporthetes lunensis* and *Pachycrocuta brevirostris*). The morphological comparisons (including multivariate morphometric analyses) enable a clear distinction among these taxa and support the attribution of the studied material to *Pliocrocuta perrieri.* The genus *Pliocrocuta* is currently considered monotypic, after the revision by Werdelin and Solounias (1991), who synonymized one genus with *Pliocrocuta* and three species with *Pliocrocuta perrieri*. Further revision is probably still required, as shown by the recent synonymization of the problematic *Crocuta sivalensis* (Falconer, 1867) to *Pliocrocuta perrieri* (Werdelin and Lewis, 2012). The morphological characterization of *Pliocrocuta perrieri* provided in this dissertation contributes to clarify the identity of this species. Chapter 5 further reports on the enamel microstructure of the studied Iberian specimens of *Pliocrocuta perrieri*, which display the zig-zag pattern characteristic of durophagous forms (Howell and Petter, 1980; Werdelin and Solounias, 1991), similarly to both extant and extinct bone-cracking hyaenas such as *Crocuta* or

Adcrocuta (Ferretti, 2007; Tseng, 2012). The zig-zag pattern was reported to be present in the p4 and m1 of *Pliocrocuta perrieri* in the appendix of Tseng (2012), but not commented further by this author in the results and discussion. Chapter 5 is the first work to confirm this pattern in the whole set of upper premolars (P2-P4) of *Pliocrocuta* (displayed in the three studied skulls) and discuss its relationship with a durophagous diet.

In turn, in Chapter 9 the internal cranial morphology of the aforementioned specimens of *Pliocrocuta perreri* is described, with emphasis on the frontal sinuses and the brain. A complete posterior elongation of the frontal sinuses in all the extinct bone-cracking hyenas was hinted by Joeckel (1998), when he reported (but not described) that this feature was present in *Adcrocuta eximia.* This is confirmed in chapter 9, which first provides a complete description of this feature in an extinct bone-cracking hyena. In *Pliocrocuta*, the described frontal sinuses completely overlap the braincase and are formed by two distinct regions (anterior and posterior), which differ mainly in the grade of pneumatization and number of chambers. The anterior one has smaller chambers and is more pneumatized, whereas the posterior one has larger chambers but is less pneumatized. This configuration of the frontal sinuses is similar to that in the extant bone-crackers. The brain morphology reported in chapter 9 for *Pliocrocuta* also represents the first published description of a fossil hyaenid brain, with emphasis on its external morphology and encephalization (relative brain size) compared to those of extant bone-crackers. The allometric analyses undertaken indicate that *Pliocrocuta* and bone-cracking hyenas (but not *Proteles*), like felids, display a higher degree of encephalization than other Feliformia. The brain morphology of *Pliocrocuta perrieri*, in turn, is overall similar in morphology to that of extant bone-crackers, in particular *Parahyaena brunnea*, whereas comparisons of regional brain volumes indicate that the relative development of the frontal region in *Pliocrocuta* most closely resembles the condition in both *Hyaena* and *Parahyaena*, which show a lesser development of this area as compared to extant *Crocuta*. A relatively enlarged frontal region has been linked to sociability in extant hyaenids (being most developed in the highly social *Crocuta*, and least in the solitary *Proteles*; Sakai et al., 2011), and can be therefore used to infer this behavioral trait in extinct hyaenids. Based on the results reported in chapter 9, *Pliocrocuta perrieri* can be inferred to have displayed a similar social behavior to *Parahyaena* and *Hyaena*, which are solitary scavengers that can gather in small groups of up to 10 members. This contradicts some previous authors, who considered that the abundance of this species in Villafranchian sites (Antón et al., 2006; Tseng et al., 2013) and the age-specific mortality pattern represented in the sites (Tseng et al., 2013) suggested a more gregarious behavior (similar to that of the extant *C. crocuta*) for *Pliocrocuta perrieri*.

11.1.3. *Pachycrocuta*

Various aspects of this well-known hyaenid genus from the Pleistocene are discussed in this dissertation, including taxonomy (chapters 6 and 8) and paleobiology (chapter 7). Chapter 8 deals on the taxonomic authority (authorship) of *Pachycrocuta brevirostris*, the type and only species of the genus. When reviewing the classical literature of this species, we discovered that the customary ascription of the original description of this species to "Aymard, 1846" was based on an inexistent publication. This is explained in greater detail on chapter 8, where it is also indicated that the species was indeed erected by Gervais (1848-1852), in a work published along several years, the description of the species corresponding to 1850. Thus, the correct author for *Pachycrocuta brevirostris* is "Gervais, 1850". Even if this is a minor nomenclatural issue, it should serve as a warning to the widely disseminated practice of copying taxonomic authorities from one work to another without consulting the primary literature—especially considering the current facilities to access digitally the classical literature that is already on the public domain.

In chapter 8, the hyaenid material from Cueva Victoria is described and compared in detail, being attributed to *Pachycrocuta brevirostris*. The presence of this taxon in Cueva Victoria was first mentioned by Pons-Moyà and Moyà-Solà (1978), who merely described two P3. However, the whole assemblage of this taxon had not been previously published. The confirmation that this material belongs to *Pachycrocuta brevirostris* has some implications for the behavior of this species and the origin of the whole fossil assemblage of this site, given previous suggestions that Cueva Victoria might have been a hyena den (Pérez-Cuadrado and Ferrández, 1992; Gibert et al., 1992, 1993, 2006). The described material generally fits well in both size and shape with other specimens of *Pachycrocuta brevirostris* from the European late Villafranchian (Moullé, 1992; Turner and Antón, 1996; Turner, 2001; Galobart et al., 2003; Kahlke, 2006; Madurell-Malapeira et al., 2009; Palmqvist et al., 2011), except for some details of the m1 occlusal morphology (presence of a reduced and vestigial metaconid, number of talonid cuspids, paraconid-protoconid proportions), which are lacking in some specimens from this site. This indicates that the check tooth morphology of this species is less homogeneous than previously assumed (Howell and Petter, 1980; Werdelin and Solounias, 1991; Turner and Antón, 1996; Galobart et al., 2003; Turner et al., 2008; Werdelin and Lewis, 2010), being ascribable to intraspecific variation because the presence/absence of each of these traits varies from one individual to another without a consistent pattern.

Finally, in chapter 7 the paleoecology of *Pachycrocuta* is revisited on the basis of the taphonomical data recorded on the herbivore remains from the various layers of the Vallparadís Section. This study reveals a bias in bone preservation (in favor of large long bones) and a clear bone consumption pattern produced by *Pachycrocuta brevirostris*, similar to that previously documented in other European localities, such as Venta Micena (Spain; Arribas and Palmqvist, 1998; Espigares, 2010), Colle Curti (Italy; Mazza and Ventra, 2011) and Untermassfeld (Germany; Kahlke, 2006). These large bone-accumulations made by *Pachycrocuta* fit with the scavenging habits inferred for this species (Palmqvist et al., 2011). Chapter 7 also points out the probable competition for resources (carcasses) that took place between *Pachycrocuta* and early European populations of *Homo* during the late Villafranchian and Epivillafranchian of Europe. This competition with *Homo* populations would have been caused by the scavenging strategies that, according to some authors (Martínez-Navarro and Palmqvist, 1995, 1996; Arribas and Palmqvist, 1998; Palombo, 2014), humans developed to assure food acquisition in temperate environments, especially during winter.

11.1.4. *Crocuta*

Chapter 10 focuses on two Pleistocene Eurasian *Crocuta* species (*Crocuta spelaea* and *Crocuta ultima*), by describing and comparing their brain volume and morphology with that of other bone-crackers, especially the extant *Crocuta crocuta,* on the basis of 3D models of the brain endocast derived from CT scans. The brain morphology displayed by the studied endocasts of *Crocuta spelaea* and *Crocuta ultima* is similar to that of extant hyaenids, especially the living *Crocuta crocuta.* Despite this expected similarity, the three studied endocasts lack the frontal development of the brain that is characteristic of extant *Crocuta crocuta,* and display instead similar values to those of *Hyaena*, *Parahyaena,* and *Pliocrocuta* (chapter 9). These results, similar to those documented for *Pliocrocuta* (chapter 9), suggest that these two species (*Crocuta spelaea* and *Crocuta ultima*) display an equally developed social behavior, most similar to that of the nearly solitary scavenger hyaenids *Hyaena* and *Parahyaena*. Such a solitary and scavenging behavior had been previously inferred for the European *Crocuta spelaea*, due to its morphological similarities with *Pachycrocuta brevirostris*. The latter has sometimes been considered a solitary scavenger (Palmqvist et al., 2011), although some authors have considered it as rather gregarious on the basis of the large bone accumulations generated by this species in caves (e.g., Diedrich 2006, 2007, 2011; Tseng et al.

2013). The relatively more developed frontal brain observed in extant *Crocuta crocuta* suggests that this character evolved quite late during the late Middle or Late Pleistocene in the African continent. This feature also strengthens the taxonomic distinction between the two studied extinct species, *Crocuta spelaea* and *Crocuta ultima*, and the living *Crocuta crocuta*. Previously, their distinction was only supported by differences in limb proportions, robusticity and size (Baryshnikov, 1999; García, 2003; Sauqué et al., 2017), which some authors considered insufficient to justify a distinction at the species rank (Kurtén, 1957; Werdelin and Solounias, 1991; Turner, 1984, 1990; Sardella and Petrucci, 2012). Indeed, some authors (Turner, 1984, 1990; Werdelin and Solounias, 1991) considered that the various fossil species of *Crocuta* from Eurasia would merely be local variants of the extant species, *Crocuta crocuta*, due to its plastic morphology. This is contradicted by the paleoneurological evidence reported in chapter 9, because brains are very expensive to maintain from a metabolical viewpoint, such that any investment in brain size increase during evolution must represent an advantage in terms of fitness (Dunbar, 1998), or else it would be readily counter-selected. Therefore, a greater development of the frontal region of the brain in *Crocuta crocuta* can be hardly considered a plastic feature and must be considered instead an autapomorphy of this species, most likely related to social behavior, thereby strengthening its distinction at the species rank from the extinct *Crocuta spelaea* and *Crocuta ultima.*

11.2. Durophagy

As explained in section 1.1.3 of the Introduction, durophagy is the ability of animals to consume hard and resilient food items, such as hard shells, exoskeletons or bones. The adaptations required by this type of diet in carnivorans include a robust craniodental morphology with a raised and dome-like frontal region of the cranium, enlarged areas for the attachment of masticatory muscles, well-developed frontal sinuses, buccolingually enlarged premolars, and microstructurally reinforced tooth enamel (Joeckel, 1998; Stefen, 1999, 2001; Stefen and Rensberger, 1999; Dong, 2008; Tanner et al., 2008; Tseng, 2009, 2012; Figueirido et al., 2012). Currently, hyenas almost have the monopoly of durophagy among carnivorans, although they are not the only ones that developed durophagous traits during the evolution of the group, as there are other extinct bone-crushers as well as bamboo-feeders that are considered durophagous. In the fossil record, the bone-cracking ecomorphotype evolved independently at least seven times among the Carnivora during the Cenozoic (Van Valkenburgh, 1999; Wang et al., 1999; Van Valkenburgh, 2007; Tseng and Wang, 2011; Valenciano et al., 2016): twice in the Hyaenidae (once in *Adcrocuta* and also in the lineage leading to modern hyaenines), once in the Percrocutidae, twice in the Mustelidae (*Megalictis* and its clade, as well as *Gulo gulo* and some older relatives, such as *Eomellivora*), and twice in the Canidae (Aelurodontina and Borophagina, both included within the Borophaginae). Bamboo-feeders are herbivores that feed almost entirely on bamboo (e.g., Gittleman, 1994; Figueirido et al., 2010). The fossil record shows that this type of diet evolved independently twice: the lineage leading to the giant panda, *Ailuropoda melanoleuca* (David, 1869), within the Ursidae; and the red panda, *Ailurus fulgens* Cuvier, 1825, within the Ailuridae (e.g., Flynn et al., 2000, 2005). There are some differences between bone-crackers and bamboo-feeders, such as the position of the mandibular condyle, which is higher in the latter (Figueirido et al., 2013). This feature may be related to the fact that bone-crackers are more adapted for the large biting forces that are needed to break bones, whereas bamboo feeders are adapted to resist stress as a result of constant strong chewing (although they can also achieve large force bites; Figuerido et al., 2012, 2013).

In this dissertation, practically all of the already well-known craniodental traits related to durophagy displayed by *Hyaenictis* aff*. almerai*, *Pliocrocuta perrieri* and *Pachycrocuta brevirostris* (e.g., Howell and Petter, 1980; Werdelin and Solounias, 1991; Turner and Antón, 1996; Galobart et al., 2003; Palmqvist et al., 2011) have been described and discussed in greater detail in chapters 4, 5, and 6. The following subsections will be focused on two different traits (the frontal sinuses and the enamel microstructure) that are clearly related to durophagy and which were investigated in greater detail in this dissertation.

11.2.1. Enamel

The microstructure of the enamel (how its prisms organize in the three dimensions) has been correlated with diet in extinct and extant carnivores (Tomes, 1906; Stefen, 1997, 1999; Rensberger and Wang, 2005; Rensberger and Stefen, 2006; Ferretti, 2007). Such correlation relies on the Hunter-Schreger bands (HSBs), which are layers of prisms that decussate in opposing orientation. These bands organize in three major types among carnivores (Stefen, 1997, 1999): undulating, acute-angled and zig-zag. These types, defined by Stefen (1997), were based on the approximate angles of the enamel bands, measured as the angle between the boundaries of a given enamel prism fold: >140º for undulating, 140–70º for acute angled, and 70–50º (or smaller) for zig-zag HSBs. Each type indicates different degrees of durophagous adaptation, the zig-zag type being the most suitable for this dietary behavior and present in extant hyaenines (Ferretti, 2007): *Crocuta*, *Hyaena* and *Parahyaena.* This pattern also evolved convergently in borophagine canids (Stefen, 1999; Rensberger and Wang, 2005; Tseng, 2011).

Extant hyaenines are considered durophagous based on their dietary behavior, and in further agreement with multiple of their craniodental features (Werdelin, 1989; Werdelin and Solounias, 1991; Joeckel, 1988; Rensberger, 1999). However, fossil forms that belong to ecomorphotypes other than 5 and 6 (Werdelin and Solounias, 1996) where generally considered not to display durophagous adaptations until HSB studies confirmed that some of these genera, such as *Thalassictis, Ictitherium,* and *Chasmaporthetes*, displayed highly reinforced enamel (Ferretti, 1999, 2007; Tseng et al., 2011; Tseng, 2012). Ferretti (2007) and Tseng (2012) combined the previously known information on bone-cracking adaptations with HSB studies in hyaenids to clarify when these adaptations appeared in the fossil record. In particular, Ferretti (2007) showed that the most resilient enamel appeared in hyaenids from ecomorphotype 6, such as *Adcrocuta* or *Pachycrocuta*, although hyenas from ecomorphotypes 3 and 4 also had an enamel microstructure suitable for bone-crushing. This author also suggested a progressive evolution of this feature in hyaenids, from the normal undulating microenamel pattern in the basal forms, such as *Protictitherium*, to the hard and resilient zig-zag enamel pattern in the most derived forms, such as *Crocuta* or *Hyaena,* with intermediate forms between them. In turn, Tseng (2012) showed that species from ecomorphotype 4 generally had, with the exception of the p4 in *Chasmaporthetes*, less resilient enamel than the basal forms belonging to ecomorphotype 3, such as *Thalassictis* or *Ictitherium*, thus contradicting Ferretti's (2007) hypothesis that the enamel microstructure only was strengthened during hyaenid evolution. Tseng (2012) concluded that enamel microstructure is quite plastic from an evolutionary perspective, such that the presence of the zig-zag pattern in the enamel of a given species would clearly reflect its durophagous habits (rather than phylogenetic constraints). Chapters 4 and 5 show that an enamel microstructure suitable for bone-cracking was already present in *Pliocrocuta*, the putative ancestor of *Pachycrocuta*, as well as in another member of ecomorphotype 4 (*Hyaenictis*), at least to the same extent as in *Chasmaporthetes*. This type of enamel microstructure in *Pliocrocuta* is not unexpected, as it fits perfectly with other durophagous traits present in this species and other members of its lineage. In contrast, the new enamel data reported for *Hyaenictis* (chapter 4) is more relevant for several reasons. First, it increases the number of known species with dental adaptations to durophagy, which is particularly relevant if it is considered that the dietary habits of ecomorphotype 4 had not been exclusively related to durophagy (Werdelin and Solounias, 1996). The second implication of this finding is that the appearance of this this kind of enamel microstructure in ecomorphotype 4 is pushed back in time from the Pliocene (*Chasmaporthetes lunensis;* Tseng, 2012) to the Vallesian (*Hyaenictis* aff. *almerai*).

It remains to be ascertained whether the zig-zag pattern of *Hyaenictis* was inherited from its ancestors or developed independently in this genus. The former hypothesis is only supported by the fact that the zig-zag enamel pattern is already present in multiple lower teeth of many previous species (Tseng, 2012), such as *Ictitherium* spp. (p2–m1), *Thalassictis* spp. (at least p4 and m1) and *Hyaenictitherium wongii* (p2–m1). The second hypothesis mentioned above (i.e., the reacquisition of a zig-zag enamel pattern in *Hyaenictis*) appears more likely. This is supported by the fact that a heavily reinforced enamel is not present in its putative ancestor, *Lycyaena* (Tseng, 2012), despite the fact that the oldest member of this genus, *Lycyaena crusafonti*, has several other durophagous traits in the dentition, and is the most durophagous hyena from ecomorphotype 4 (Kurtén, 1976; Werdelin, 1988; Werdelin and Solounias, 1991; Werdelin et al., 1994), other than the new *Hyaenictis* material (chapter 4). The plasticity of this feature (Tseng, 2012) suggests that the basal hyaenid of ecomorphotype 4 *Lycyaena* lost the zig-zag pattern in its tooth enamel, despite the retention of long-term adaptations to durophagy (chapters 4 and 11), due to a lack of use associated to a hypercarnivorous diet. *Hyaenictis* might have reacquired the zig-zag enamel as a consequence of a readaptation to a durophagous diet, which would have been facilitated due to the less plastic above-mentioned adaptations to durophagy inherited from *Lycyaena* (chapters 4 and 11). The implications of this hypothesis for the evolutionary history of bone-cracking hyenas will be discussed below.

11.2.2. Frontal sinuses

Well-developed frontal sinuses are common among hyaenids. Their development can be ascertained and roughly quantified based on the external morphology of the skull, but CT scans are required for a deeper analysis. This feature appeared quite early during the diversification of hyaenids, although with different degrees of development. *Adcrocuta* has been shown as the oldest hyaenid with the frontal sinuses totally elongated backwards, covering the whole braincase (Joeckel 1998; Vinuesa et al., 2013), and all of the large hyenas from ecomorphotypes 4, 5 and 6 that have been studied so far also display totally elongated frontal sinuses (chapter 9; Joeckel, 1998; Tseng et al., 2011). The enlargement of the frontal sinuses must have taken place during the middle Miocene, because species from ecomorphotype 3, such as *Hyaenictitherium* or *Ictitherium*, already show somewhat enlarged frontal sinuses, even if they do not fully cover the braincase (Joeckel, 1998). In other carnivorans, this trait is quite rare, and only some borophagine canids and ursids display it (Davis, 1964; Werdelin, 1989), albeit to a lesser extent than in hyaenids (Werdelin 1989; Joeckel 1998; Tseng and Wang, 2010). Borophagine canids are considered opportunist scavengers with bone-cracking adaptations (Werdelin, 1989), although several controversies persist about their feeding behavior (Van Valkenburgh et al. 2003; Andersson 2005). The two species of this group that show a greater development of this character are *Borophagus dudleyi* White, 1941 and *Borophagus diversidens* Cope, 1892 (Tseng and Wang, 2010). Among ursids, this feature is present in the giant panda (Davis, 1964), *Ailuropoda melanoleuca* (David, 1896), which subsists on an herbivorous durophagous diet consisting mainly of tough bamboo shoots (Schaller et al., 1985, 1989).

The precise function of expanded and elongated frontal sinuses among carnivorans, as previously discussed in chapter 9, is somewhat unclear. Functional hypotheses have been proposed that relate this morphology to shock dissipation, brain cooling, olfaction, and/or maximization of muscle attachment areas, although none of these explanations is entirely satisfactory (Joeckel, 1998; Werdelin, 1989). The most convincing hypothesis is that the enlargement of the sinuses helps to dissipate ant resist the stresses imposed on the skull (not necessarily due to masticatory muscles forces), by acting as a buttress between the neurocranium and the splanchnocranium, and thereby resisting any dorsal torque imposed on the face during bitting (chapter 9; Joeckel, 1998). Along this line of reasoning, several studies have tested the resistance of the skull and the sinuses on different species, such as *Crocuta* (Tanner et al., 2008), *Chasmaporthetes* (Tseng et al., 2011) and borophagine canids (Tseng and Wang, 2010), with varied results, explained ahead. The first study (Tanner et al., 2008) made a comparison of different skull structures in *Crocuta*: the real one with elongated frontal sinuses, one with the sinuses completely filled with bone, and another replacing the frontal sinuses with a high sagittal crest. The results showed that the most efficient structure is the one currently displayed by *Crocuta*, as it ensures a better and even distribution through the skull of the bite stress without losing much bite force. The second study (Tseng et al., 2011) compared the skull resistance of *Chasmaporthetes* and *Crocuta,* arriving to the conclusion that *Chasmaporthetes* skull resistance is slightly lower than that of *Crocuta*, and that it might have been useful for *Chasmaporthetes* to resist the forces of the powerful gripping bite used to hunt instead of cracking bones. The third study (Tseng and Wang, 2010) compared the resistance in the skull to bite stress in six different canid species, including some bone-crackers (borophagines) and some meat-eaters (such as wolves). This study showed that bone-crackers have the bite stresses more evenly distributed through the skull, as in the case of hyaenids.

Tseng and Wang (2010) performed another analysis comparing the resistance of these skulls to muscle-directed bite stresses, depending on the main muscle that exerts the force (the temporalis or the masseter). The results showed that meat-eaters are more efficient during a masseter-driven bite (used in hunting), whereas bone-crackers are more efficient during a temporalis-driven bite (used in bone cracking). The conclusion of this work thus reinforces further Tseng et al.'s (2011) hypothesis that the development of the frontal sinuses in *Chasmaporthetes* was biomechanically most advantageous during hunting. In any case, all the studies mentioned above agree that the development of the frontal sinuses along the sagittal crest improves the stress dissipation in the skull.

Currently available paleontological data indicate that developed frontal sinuses began to develop early in the evolutionary history of hyaenids, probably being already present in genera from ecomorphotype 3 such as *Ictitherium* and *Thalassictis* (Joeckel, 1998), as an adaptation to the durophagous diet of these species (as evidenced in the previous section). Unlike enamel microstructure, this feature does not seem to be plastic in evolutionary terms, as it is present in all of the derived hyaenids evolved from ancestors that possessed this feature (such as *Adcrocuta*, *Hyaenictis, Pliocrocuta perrieri*, or *Chasmaportetes lunensis*, see chapters 4 and 9; Joeckel, 1998; Antón et al., 2006). Given the lack of documented reversals for this feature, it looks more like a long-term adaptation that was only subsequently lost in *Proteles* (Joeckel., 1998), together with many other features (such as the dentition), if at all (since the condition from which the *Proteles* lineage evolved is uncertain; Werdelin and Solounias, 1991; Werdelin and Sanders, 2010). The assumption that, once acquired, long frontal sinuses cannot be readily lost is supported by the fact that derived hyenas from ecomorphotype 4 have retained this feature, despite having a diet focused on hypercarnivorism (Kurtén and Werdelin, 1988; Werdelin and Solounias, 1991, 1996; Antón et al., 2006; Tseng et al., 2013). In fact, available data suggests that the biomechanical advantages of this feature (related to stress dissipation and bite force), even if originated as an adaptation to a bone-cracking diet, were subsequently co-opted for other types of diet in other taxa, such as *Chasmaporthetes*, more adapted to active hunting (Tseng et al., 2011). This is also clearly illustrated by extant *Crocuta*, in which this feature is arguably advantageous for bone consumption and active hunting alike. It is likely that the retention of this character in the hunting-hyenas clade allowed the *Hyaenictis* lineage to re-evolve a more durophagous diet (see discussion in chapters 4 and 11). The implications of these data for the evolutionary history of hyaenids are further discussed below in section 12.3.

11.3. Paleoneurology

Paleoneurological studies in fossil carnivorans had never focused on hyaenids. Two main approaches have been employed in this dissertation. The first consist of the study of encephalization (relative brain size) in extinct species compared to that of extant ones, with the aid of allometric techniques that take body size scaling into account. This approach, widely applied to Plio-Pleistocene hominins and other extinct primates, has also been successfully used in other groups, such as carnivorans, with interesting results (e.g., Finarelli and Flynn, 2009). The other main approach followed here to study brain evolution is focused on external brain morphology, as previously applied to other fossil carnivorans (Radinsky, 1969, 1971, 1975, 1977).

Encephalization degree has been linked to behavioral flexibility as well as sociability in several groups, such as primates (e.g., Byrne and Whiten, 1988; Barton and Dunbar, 1997; Kay et al., 1997; Dunbar and Schultz, 2007; Sears et al., 2008), cetaceans (Marino et al., 2004), birds (Nealen and Ricklefs, 2004), and carnivorans (Finarelli and Flynn, 2009; Swanson et al., 2012), especially canids (Finarelli and Flynn, 2007; Finarelli, 2008) and hyaenids (Sakai et al., 2011). These works cited above have been discussed in greater detail in chapters 9 and 10. Finarelly and Flynn (2009) grouped carnivorans according to their degree of encephalization, showing that felids, canids, and ursids are among the most encephalized carnivorans. According to this analysis, hyaenids would resemble basal carnivorans in terms of encephalization. In contrast, chapters 9 and 10 show that not all hyaenids are comparable in this regard. In particular, extant hyaenines possess a similar degree of encephalization to felids, being considerably more encephalized than *Proteles*, which falls within the range of encephalization of non-felids Feliformia. This suggests that, after the divergence of Protelinae and Hyaeninae, there was a considerable brain size increase in hyaenines—or, alternatively, that *Proteles* displays a reduced brains size as compared to its last common ancestor with hyaenines. The lack of brain size estimates for Miocene hyaenines, such as *Adcrocuta* or *Chasmaporthetes*, and for basal hyaenids, such as *Protictitherium* and *Plioviverrops*, does not allow us to more conclusively ascertain the evolution of this trait in hyaenids.

With regard to the evolution of brain morphology in carnivorans, the first studies where performed by Radinsky (1969, 1971, 1975, 1977) on the basis of endocasts. Radinsky's (1969) paper was focused on the evolution of the brain in canids and felids, with particular emphasis on the time of origin of certain areas and sulci in the various families. Radinsky (1971), in turn, was more focused on carnivorans as a whole, evidencing that, despite the fact that all basal carnivorans had a similar brain morphology, the cruciate sulcus evolved in parallel among the various families. Radinksy (1975) focused again on felid brain evolution, but more in-depth. In turn, Radinksy (1977) investigated the evolution of the brain in Oligocene and basal Miocene carnivorans. After these seminal studies, no further works have focused on the external brain morphology of fossil carnivorans until the two studies included in this dissertation about *Pliocrocuta* and *Crocuta* (chapters 9 and 10, respectively). These chapters show that, on morphological grounds, the brains of *Pliocrocuta* and the extinct Eurasian *Crocuta* were more similar to those of *Hyaena* and *Parahyaena*, and differ from the extant African *Crocuta* in the lesser development of the frontal cortex.

Considering the small amount of information available on basal hyaenid brain morphology, the evolution of this relevant organ is rather unknown. Basal carnivorans related to hyaenids, the viverrids, and herpestids, have a rather simple brain in terms of morphology (Radinsky, 1971). As an example, the brain of the herpestid *Herpestides antiquus* (early Miocene of Europe) only has the ectolateral and lateral sulcii marked on the endocasts (Radinsky, 1971), and the cerebellum+brain stem is almost the same size as the cerebrum. The oldest available endocast for hyaenids is that of *Adcrocuta* (Appendix), which already shows a greater number of sulcii (8) in its large cerebrum, with the cruciate already formed, but being small and located frontally, similar to that of *Proteles*—supporting the idea that *Proteles* has the most primitive brain of all extant hyaenids (Appendix). This fact tends to favor the view that *Proteles* is primitively less encephalized than hyaenines (rather than secondarily less encephalized, see above), although additional evidence from the fossil record would be required to test this hypothesis. Unfortunately, there are no brain data from the time span between *Adcrocuta* and the basal hyaenid hypothetical brain morphotype, which would have arguably been similar to that of the fossil herpestid *Herpestides*. This is because there are no available hyaenid endocasts of the genera *Protictitherium* or *Plioviverrops* from the early Miocene yet. These genera would be expected to have more primitive brains than *Adcrocuta*, with a smaller number of sulci marked, and maybe with the cruciate sulcus not developed. It should be also taken into account that *Adcrocuta* coexisted with many other hyaenids during the late Miocene, such as *Hyaenictis*, *Ictitherium* or *Hyaenictitherium*, for which there are no available endocasts. These other genera might have possessed similar brains to *Adcrocuta* (and *Proteles*), but this remains to be ascertained based on fossil evidence. The next available endocast is dated to the Pliocene, as represented by *Pliocrocuta* (chapter 9), which already shows a more complex brain than *Proteles* and *Adcrocuta*, similarly to *Hyaena* and *Parahyaena.* Last, but not least, the extinct *Crocuta spelaea* and *Crocuta ultima* from Eurasia

(Chapter 10) differ from the extant *Crocuta crocuta* in the size of the frontal cortex, in a similar way that *Hyaena* and *Parahyaena* do, suggesting that an enlarged frontal cortex is only present in the African lineage of *Crocuta*. A detailed analysis of the brain morphology of *Chasmaporthetes* could reveal and independent evolution of a more developed frontal cortex in this genus, which like *Crocuta* is considered a pack-hunter due to its hypercarnivorous and cursorial traits (similar to those of *Lycaon*), being the most extreme representative of ecomorphotype 4 (Antón et al., 2006).

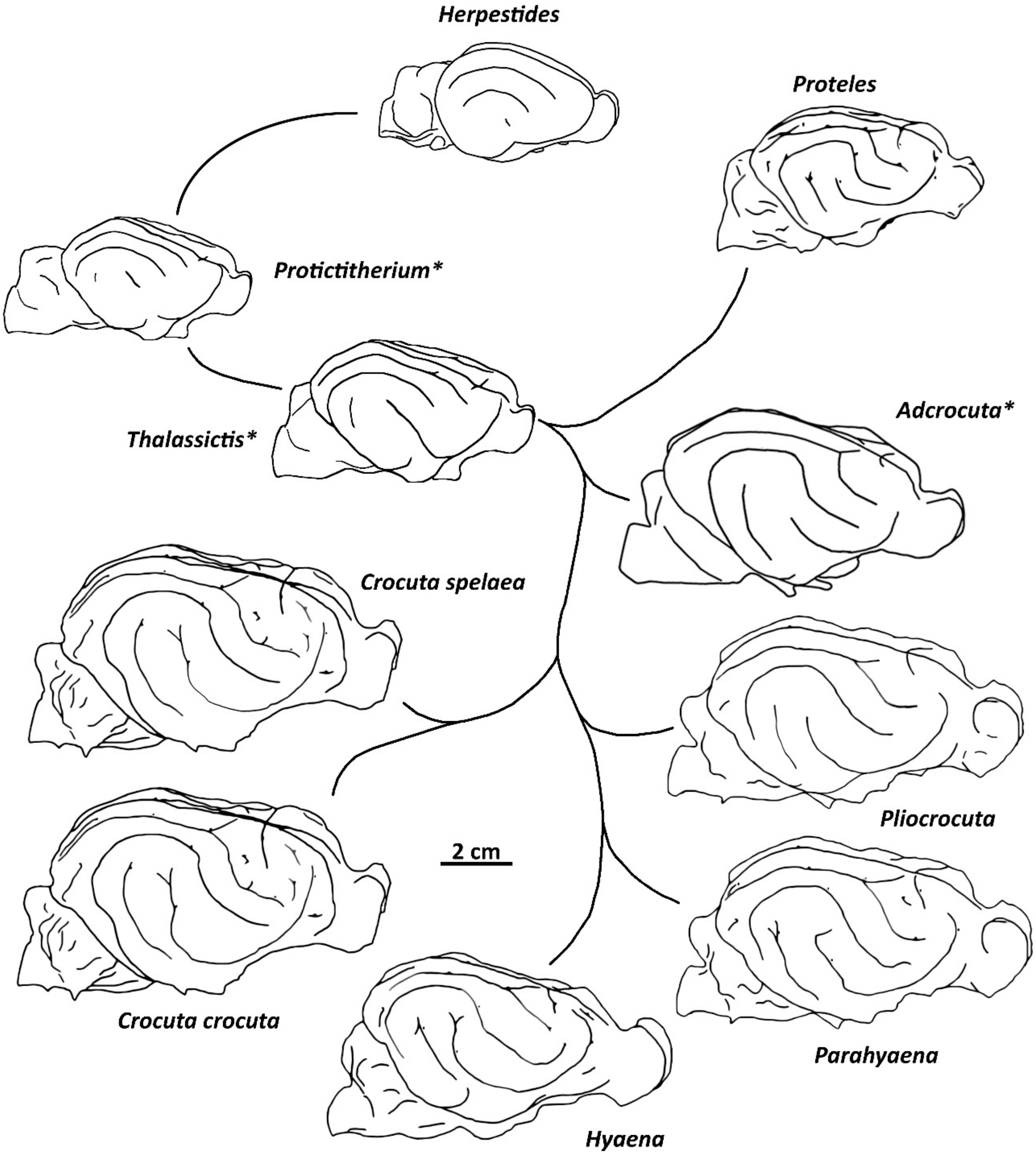

Figure 11.1: Brain morphology evolution in the family Hyaenidae. Asterisks denote hypothetical brain morphologies, according to the known data of primitive and derived species (see main text of the Discussion for further details). *Herpestides* brain morphology is extracted from Radinsky (1971).

In summary (Fig. 11.1), early hyaenids displayed a small simple brain, which became larger and more complex during the Miocene, as shown among other features by the appearance of the cruciate sulcus by this time. Subsequent Pliocene and Pleistocene hyaenids, most of them belonging to the bone-cracking ecomorphotype (with the exception of *Chasmaporthetes lunensis*), already had complex brains, with a large cerebrum and a well-developed frontal cortex. However, the extant African *Crocuta crocuta* is the only known hyaenid known to have developed an enlarged frontal cortex (exclusive of Eurasian species of the same genus), suggesting that this feature might be autapomorphic of this species.

11.4. Evolutionary history

Taking into account the above-mentioned new data on durophagy and paleoneurology in hyaenids, the origin and evolution of bone-cracking hyenas is revisited below. Several relatively recent reviews on this topic are available (Tseng and Wang, 2007; Turner et al., 2008; Werdelin and Sanders, 2010; Tseng et al., 2013), although they only considered the Eurasian and African species. North American species are in need of review (Kurtén and Werdelin, 1988; Werdelin and Solounias, 1991). Current hypotheses on the evolutionary history of the family Hyaenidae have been already summarized in the Introduction (section 1.2.4). Some of the new findings reported here (see below) support some of the already established hypotheses (e.g., with regard to the development of the frontal sinuses), whereas others challenge some of them and offer new alternate hypotheses (e.g., the presence of the complex zig-zag pattern in *Hyaenictis*).

As previously stated, the earliest hyaenid genera, *Protictitherium* and *Plioviverrops*, were small carnivorous/insectivorous forms, similar to extant herpestids and viverrids. These genera are first recorded during the early Miocene (MN4; Turner et al., 2008) and probably originated in Western Europe (Werdelin and Solounias, 1991; Werdelin and Solounias, 1996; Turner et al., 2008). During the middle Miocene (MN7+8), the first medium-sized derived forms (ecomorphotype 3), such as *Thalassictis*, appeared in the fossil record, probably evolved from *Protictitherium*, also in Western Europe (Werdelin, 1988a; Werdelin and Solounias, 1991; Werdelin, 1996). Some species included in *Thalassictis* already showed incipient adaptations towards durophagy, as shown by the broadening of the dentition, the reduction of the posterior molars, the enlargement of the posterior premolars, the zig-zag enamel pattern, the development of the frontal sinuses, etc. (Villalta and Crusafont, 1943; Crusafont and Petter, 1969; Werdelin, 1988a; Werdelin and Solounias, 1991; Werdelin, 1996, Tseng, 2012). During the Vallesian (MN9–MN10), these jackal-like forms from ecomorphotype 3 became the most abundant hyenas, although two other genera from ecomorphotype 3, *Ictitherium* and *Hyaenictitherium,* also appear in the fossil record by that time (Werdelin and Solounias, 1991; Werdelin, 1996; Turner et al., 2008). During the Vallesian, genera from other ecomorphotypes, such as *Hyaenictis* (ecomorphotype 4) or *Metahyaena* (ecomorphotype 5), also appeared, being characterized by a larger size, when compared to ecomorphotype 3 hyaenids, and more derived durophagous and/or hypercarnivorous characters (depending on the species) than those of ecomorphotype 3 (Villalta and Crusafont, 1943; Werdelin and Solounias, 1991; Werdelin et al., 1994; Werdelin, 1996; Viranta and Werdelin, 2003; Turner et al., 2008). Also, during MN10, the first hyena with well-developed bone-cracking adaptations, *Adcrocuta eximia* appears (Werdelin and Solounias, 1991; Turner et al., 2008). The precise origin of this lineage, which terminates at the end of the Turolian, is uncertain on phylogenetic terms (Turner et al., 2008). The brain morphology (Vinuesa et al., 2013), the strengthening of the enamel (Ferretti, 2007; Tseng, 2012), and the extensive development of the frontal sinuses (Joeckel, 1998) displayed by this genus would situate its divergence at some point after the beginning of enlargement of the sinuses and the strengthening of the enamel, but before the development of the frontal cortex (anterior to the cruciate sulcus) that is shared modern hyaenines and first displayed by *Pliocrocuta* (Chapter 9). In temporal grounds, the divergence of the *Adcrocuta* lineage would be placed around the divergence of *Proteles* from the remaining extant hyaenids (i.e., hyaenines), which has been estimated by molecular analyses at ca. 10.6 Ma (Koepfli et al., 2006). According to this, *Adcrocuta* might have originated during the early late Vallesian (MN10) in Europe (Werdelin and Solounias, 1991; Turner et al., 2008) from a smaller form, such as *Thalassictis, Ictitherium* or *Hyaenictitherium*, which have an intermediate development of the frontal sinuses (Joeckel, 1998). An origin of *Adcrocuta* from *Hyaenictitherium* can be ruled out on paleobiogeographic grounds, because, when the former originated, *Hyaenictitherium* was practically restricted to Asia, unlike the other two other genera mentioned above (Werdelin 1988a; Turner et al., 2008; Tseng et al., 2012). A close phylogenetic link between *Hyaenictitherium* and *Adcrocuta* is further contradicted by morphological features, because the only European representative of the former genus, *Hyaenictitherium wongii*, lacks the durophagous traits already displayed by *Hyaenictitherium hyaenoides* shortly thereafter in Asia (Tseng et al., 2012). The dental morphology of *Adcrocuta* does not give us many clues as to which of the remaining taxa, *Thalassictis* and *Ictitherium*, is the most likely ancestor of *Adcrocuta*, which already possesses all the durophagous derived characters in the cheek teeth: broad premolars with small cuspids, loss of M2 and m2, great reduction of M1 and of m1 talonid, reduction/loss of the m1 metaconid, enlargement of the m1 protoconid to the level of the paraconid, and zig-zag enamel pattern (Howell and Petter, 1985; Werdelin and Solounias, 1991; Tseng, 2012). *Adcrocuta* also displays a unique character, the reduction of the P4 protocone, which is not present to any extent in *Thalassictis* or *Ictitherium* (Werdelin 1988a, b)*. Thalassictis* appears as a most likely ancestor, as it has a more derived m1, with smaller talonid and metaconid than *Ictitherium* (Werdelin, 1988a, b; Werdelin and Solounias, 1991). Furthermore, *Thalassictis* has larger premolars, and more developed durophagous adaptations in the skull (deeper masseteric fossa, a more robust mandible, and wider zygomatic arches) than *Ictitherium*, as previously noted by some authors (Villalta and Crusafont, 1943; Werdelin, 1988a, b; Werdelin and Solounias, 1991).

The origin of extant hyaenines and the *Chasmaporthetes* lineage has been the subject of a long-standing debate during the last decades (e.g., Ficarelli and Torre, 1970; Howell and Petter, 1985; Werdelin and Solounias, 1991, 1996; Turner et al., 2008). The current consensus is that both groups evolved independently from *Hyaenictitherium hyaenoides*, which, overall, has most derived durophagous features (Werdelin and Solounias, 1991, 1996), with broader premolars than *Thalassictis*, and an even more derived m1 that has equally large protoconid and paraconid. The latter character is not fully developed in *Thalassictis,* in which the protoconid is still smaller than the paraconid (Villalta and Crusafont, 1943; Werdelin and Solounias, 1991). This hypothesis would be suitable, in terms of morphology and timing, for the origin of Plio-Pleistocene bone-crackers. However, the time of appearance of *Lycyaena* (MN9) and *Hyaenictis* (MN10) does not support the evolution of this group from *Hyaenictitherium hyaenoides*, as some authors suggested (Tseng et al., 2012). In fact, *Hyaenictitherium hyaenoides* first appears in the fossil record during MN11, i.e., later than the two other genera (Werdelin, 1988a; Werdelin and Solounias, 1991; Tseng et al., 2012). The *Chasmaporthetes* clade would have more likely originated from *Lycyaena*, because the latter is first recorded in MN9 and displays a mix of primitive traits (presence of m2 and large m1) and derived traits (e.g., p4 shape similar to that of *Chasmaporthetes*).

The new data reported on *Hyaenictis* aff. *almerai* in chapter 4 also casts some doubts on the interpretation that *Hyaenictitherium hyaenoides* gave rise to the Plio-Pleistocene bone-crackers, as it provides a new possible origin for the latter clade. The derived craniodental durophagous traits of *Hyaenictis* are close to those of truly developed bone-crackers, such as *Adcrocuta* (chapter 4) as well as Plio-Pleistocene bone-cracking hyenas like *Pliocrocuta perrieri* (chapter 5). These shared-derived features include, among others, the broad premolars, the small accessory cusps of the premolars, the rotation of the anterior accessory cusps in the premolars or the zig-zag pattern in the enamel microstructure. The new material of *Hyaenictis* reported in this dissertation favors the hypothesis that modern hyaenines may have evolved from *Hyaenictis*, a genus previously included within ecomporphotype 4 but which currently includes at least one species from ecomorphotype 5 (chapter 5 and subsection 11.1.1)—instead of having independently originated from *Hyaenictitherium,* included in ecomorphotype 3 (Werdelin and Solounias, 1991). There are no known representatives of the modern hyaenine lineages before MN13 (late Turolian), when *Ikelohyaena* is recorded in Africa (Werdelin and Sanders, 2010) and *Pliocrocuta* in China (Tseng et al., 2015). In turn, the only representatives of ecomorphotype 5—*Metahyaena*, *Palinhyaena* and *Belbus*, from the Vallesian (MN9) of Turkey and the Turolian (MN11–MN12) of China and Greece, respectively (Werdelin and Solounias, 1991; Werdelin and Solounias, 1996; Viranta and Werdelin, 2003)—are not very well known and their precise phylogenetic relationships are uncertain, despite being placed by cladistics at the base of the extant hyaenine clade. Some authors (Werdelin and Solounias, 1996) also situated the origin of the extant hyaenines in Asia, due to the presence there of *Metahyaena* and *Palinhyaena*, which are included in ecomorphotype 5.

Considering that *Palinhyaena* probably gave rise to *Pliocrocuta*, and (maybe) also *Ikelohyaena*, the origin of *Palinhyaena* should be addressed. The two main candidates are *Hyaenictitherium* and *Hyaenictis*. *Hyaenictitherium* appeared in Asia during the Vallesian (MN9–MN10) and spread across Eurasia and Africa during the Turolian, being also recorded in Africa during the Pliocene (Tseng and Wang, 2007; Werdelin and Sanders, 2010). In turn, *Hyaenictis* originated in Western Europe during the late Vallesian (MN10; Villalta and Crusafont, 1948; Turner et al., 2008) and spread across Europe during the Turolian (MN11–MN12; Turner et al., 2008), being last record in the African Pliocene, like *Hyaenictitherium* (Werdelin and Sanders, 2010). In terms of time, both genera could be ancestral to *Palinhyaena*; in terms of spatial distribution, *Hyaenictitherium* has a larger range, although the presence of *Hyaenictis* in both Europe and Africa suggests that it could have been present as well in southwestern Asia, as it is the most common dispersal route between Africa and Europe (through the Middle East and Egypt); in terms of morphology, *Hyaenictis* is more similar to extant hyaenines, due to its durophagous adaptations and larger size, although *Hyaenictitherium* is not much more different either in these regards.

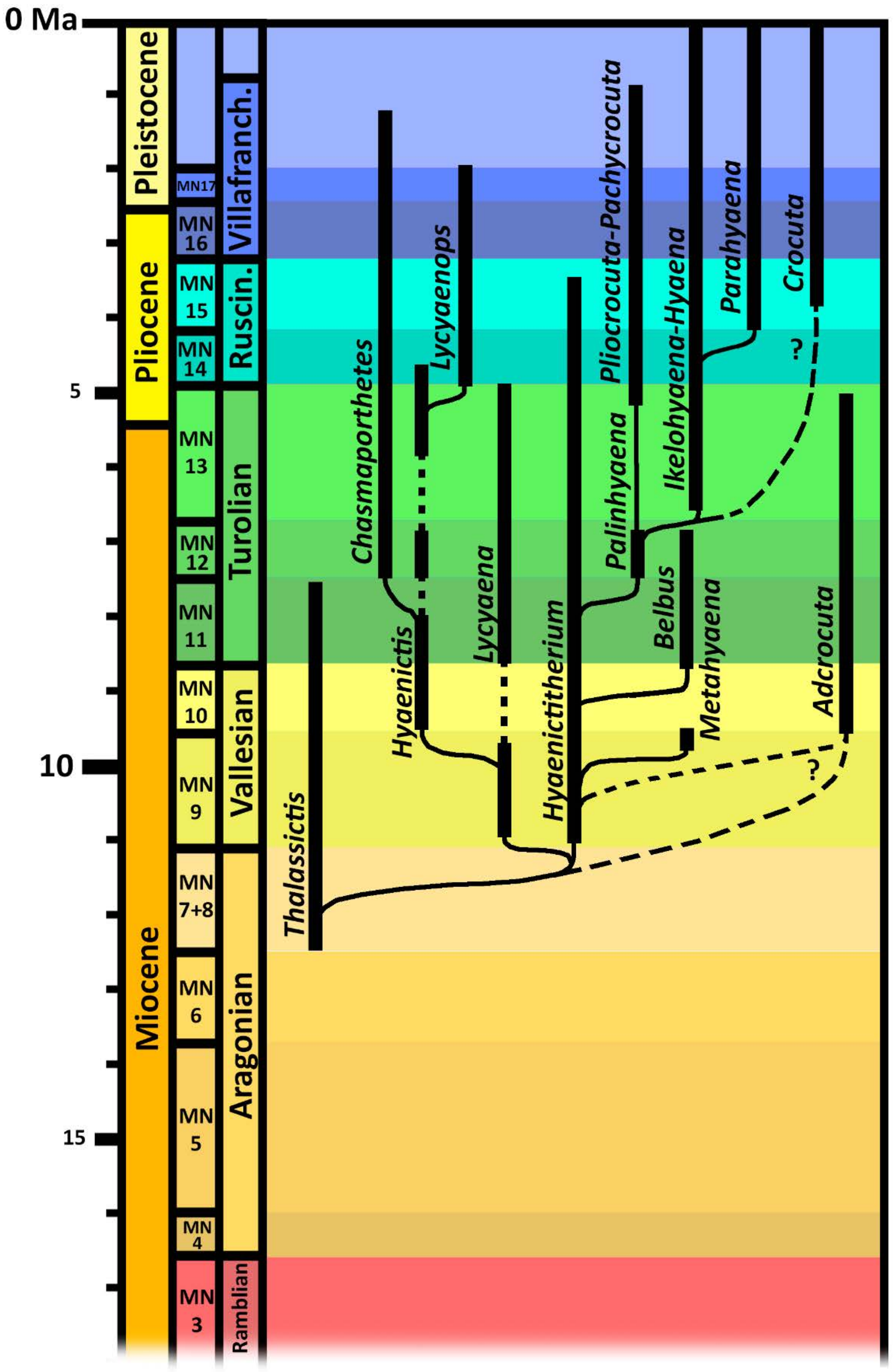

Figure 11.2: Evolutionary tree that summarizes the first scenario for the evolutionary history of the family Hyaenidae, based on the literature (see main text of the Discussion for further details). Thick solid lines denote the chronostratigraphic range of each genus (or lineage), while dotted lines denote gaps in such ranges; thin solid lines indicate divergence points based on well-established phylogenetic relationships, whereas dashed think lines accompanied by a question mark indicate more uncertain phylogenetic hypotheses.

The aforementioned facts lead to two plausible scenarios. According to the first one, already explained above (Fig. 12.1), *Palinhyaena* and derived hyaenines would have evolved from *Hyaenictitherium* during the Turolian, leading to the three major Plio-Pleistocene lineages (*Pliocrocuta*, *Hyaena,* and *Crocuta*); the durophagous lineage of *Hyaenictis* (different from that leading to *Chasmaporthetes*) would be a dead-end lineage that could not compete with the successful *Adcrocuta*. The second scenario (Fig. 12.2) is more complex, as it involves independent origins for each lineage, even if it appears more likely in the light of the new data reported in this dissertation. According to this alternate scenario, the lineages of *Pliocrocuta* and *Hyaena* would have originated independently from the same common ancestor, *Hyaenictis*, with *Palinhyaena* being a likely intermediate step between *Hyaenictis* and the clade formed by *Pliocrocuta* + *Hyaena*, leading to the extinct *Pliocrocuta* in Eurasia and to the extant *Hyaena* in African. This scenario is supported by the fact that both lineages have a combination of characters that make them very similar and closely related, as already noted by some previous authors (chapter 5; Thenius, 1966; Galiano and Frailey, 1977). This scenario is also in agreement with several features that are more derived in *Hyaenictis* than in *Hyaenictitherium* (larger size, more reduced M1, broader premolars, broader and lower p4 distal accessory cusp, and more reduced m1 talonid), suggesting that *Hyaenictis* is a more likely ancestor of the Plio-Pleistocene bone-crackers. As previously stated, the idea that *Hyaena* and *Pliocrocuta* are more closely related to each other than to *Crocuta* is not new (e.g., Thenius, 1966; Galiano and Frailey, 1977). Several features link these two genera with the exclusion of *Crocuta*: the slenderness of the P3, the morphology and size of the m1, the presence of m1 talonid and metaconid, the shorter m1 trigonid, the general shape of the cranium, and the enamel microstructure (Howell and Petter, 1980; Werdelin and Solounias, 1991; Ferreti, 2007). Considering this, it is certainly plausible that the lineages of *Crocuta* and *Hyaena* (the latter also including also *Parahyaena*, *Pliocrocuta,* and *Pachycrocuta*) evolved independently from a more primitive ancestor. This hypothesis, however, has not been supported by cladistic analyses (Werdelin and Solounias, 1991; Turner et al., 2008), in which *Hyaena, Parahyaena*, *Pliocrocuta,* and *Pachycrocuta* do not cluster together in a monophyletic clade exclusive of *Crocuta*, but sequentially branch off along the dicotomies that lead to the clade formed by *Crocuta* + *Adcrocuta*. This topology is at odds with the morphologies displayed by Plio-Pleistocene hyaenids, as well as with the molecular analysis that places *Hyaena* and *Parahyaena* in the same clade (Koepfli et al., 2006). Such discrepancies are probably caused by

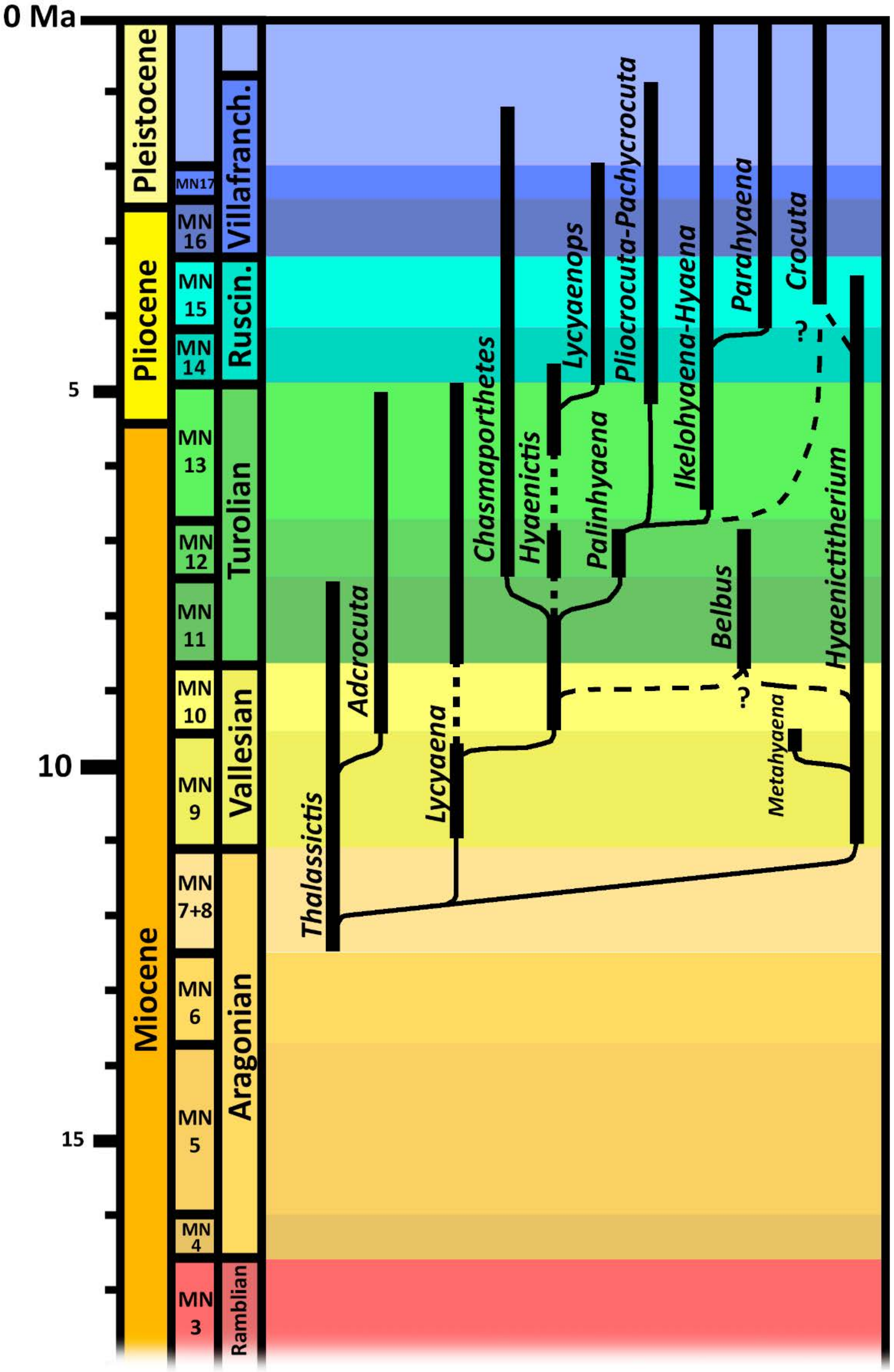

Figure 11.3: Evolutionary tree that summarizes the second scenario for the evolutionary history of the family Hyaenidae, based on the new information discussed in this dissertation (see main text of the Discussion for further details). Thick solid lines denote the chronostratigraphic range of each genus (or lineage), while dotted lines denote gaps in such ranges; thin solid lines indicate divergence points based on well-established phylogenetic relationships, whereas dashed think lines accompanied by a question mark indicate more uncertain phylogenetic hypotheses.

extensive homoplasy in multiple characters (such as the dental characters in relation to durophagous adaptations), coupled with the lack of enough phylogenetically informative characters and excessive missing data in many extinct species. These problems could be ameliorated by focusing on those extinct species that are more completely preserved as well as by adding additional characters from other functional areas (such as the morphology of the frontal sinuses and brain morphology). The incorporation of these data could hopefully result in a better resolution of the internal phylogeny of hyaenids that is also in greater agreement with the evidence available from both molecular analyses and the evidence provided by the fossil record, particularly for Plio-Pleistocene bone-cracking hyenas (Qiu, 1987; Werdelin and Solounias, 1990, 1991).

The *Crocuta* line would have originated in Africa during the Pliocene from either *Hyaenictitherium* or *Palinhyaena*. *Crocuta dietrichi,* the earliest species of the genus (MN15; Werdelin and Lewis, 2008), already displays almost all of the derived dental characters of the Hyaeninae (a fully hypercarnivorous m1 that lacks the metaconid and has a vestigial talonid, and large and broad premolars; Werdelin and Lewis, 2008), alongside *Adcrocuta*, and there are no intermediate species recorded between *Crocuta dietrechi* and either *Hyaenictitherium* and *Palinhyaena*. Subsequently, the genus *Crocuta* would have expanded towards Eurasia, where it is recorded until the Late Pleistocene (see section 1.2.4) As anticipated above, to further clarify the phylogeny of the Hyaenidae, new cladistic analyes would be required, being based on a character matrix that, besides external craniodental traits, further includes internal cranial characters. The characters that could be included in the matrix on the basis of brain morphology are the development of the sulcii, the position of the cruciate sulcus, or the enlargement of the frontal area. The overall morphology of the brain (chapter 11), if considered in a formal cladistic analysis, would likely result in *Adcrocuta* being recovered in a more basal position (Appendix 1), instead of as the sister taxon of *Crocuta* (Werdelin and Solounias, 1991; Turner et al., 2008). The latter topology results from several putative synapomorphies recovered by the analysis (such as the loss of the m1 talonid and metaconid; Werdelin and Solounias, 1990, 1991), which might arguably be alternatively considered homoplasies, particularly in the light of the considerable temporal gap between the two genera as well as the multiple morphological differences between them. This exemplifies why brain morphology is a potentially useful source of phylogenetic information that, thus far, has not been adequately explored from a phylogenetic perspective. For example, this is illustrated by the development of the frontal area, which helps to distinguish between the extant *Crocuta crocuta* and the fossil Eurasian species (chapter 10 and section 11.3), such as *Crocuta spelaea*.

Previously, these species were only distinguished on the basis of limb proportions, size, and robusticity of the skeleton (Baryshnikov, 1999; García, 2003; Sauqué et al., 2017) and some authors considered these differences insufficient to justify a distinction at the species rank (Kurtén, 1957; Werdelin and Solounias, 1991; Turner, 1984, 1990; Sardella and Petrucci, 2012). Similarly, a detailed study of brain morphology (Chapters 9 and 10) in certain hyaenid genera, such as *Hyaenictitherium* or *Thalassictis*, might potentially contribute to clarify when the hyaenine morphology appeared and thus, to better resolve their phylogenetic relationships. In turn, the development of the frontal sinuses (chapters 9 and 10) might be useful to unravel the phylogenetic relationships of *Ictitherium*, *Thalassictis,* and *Hyaenictitherium*, which originated when this feature had not fully evolved yet (Joeckel, 1998; section 12.2.2). Another potentially useful character from a phylogenetic viewpoint would be the development of the tympanic bullae (Semenov, 2008; Fraile, 2016), which a priori appears most helpful with regards to the phylogenetic relationships of the basal hyaenids, *Plioviverrops* and *Protictitherium*, as well as more derived taxa such as *Ictitherium*, *Thalassictis,* and *Hyaenictitherium*, as this feature, like the frontal sinuses, evolved during the late Miocene (MN9-MN10). Finally, other inner cranial features not yet studied, such as the nasal fossa or the cranial nerve canals, might also have some phylogenetic potential. Future studies focused on these topics and anatomical areas in hyaenids will hopefully shed new light on the phylogeny of the group by providing additional data to perform more comprehensive phylogenetic analyses that will definitively help to settle the debates discussed in this dissertation about the evolutionary history of this family in the Neogene and Quaternary of the Old World.

Chapter 12. Conclusions

The main conclusions of this dissertation are summarized below, grouped around the three main topics commented on the Discussion above: taxonomy (conclusions 1-3), paleobiology (conclusions 4-8) and evolution (conclusion 9).

1. Previously unpublished hyaenid material (including a skull) from Ronda Oest Sabadell (MN10, late Miocene) in NE Iberian Peninsula is described and tentatively assigned to *Hyaenictis* aff. *almerai* (chapter 4). This material is the most complete of this poorly-known genus in the old world and therefore greatly improves the knowledge about its dietary adaptations (see below).
2. Previously unpublished hyaenid material (including three crania) from Villaroya (2.6 Ma; La Rioja) and La Puebla de Valverde (2.0 Ma, Teruel) in the N and E, respectively, of Iberian Peninsula is described and assigned to *Pliocrocuta perrieri* (chapter 5). Morphological and morphometric comparisons indicate that this species can be readily distinguished on external morphological (dental) grounds from other Plio-Pleistocene hyenas on the basis of dental proportions.
3. Mostly unpublished hyaenid material (basically dental remains) from Cueva Victoria (0.9–0.8 Ma, late Early Pleistocene) in SE Iberian Peninsula is described and assigned to *Pachycrocuta brevirostris* (chapter 6). It is shown that this species displays a higher degree of intraspecific variability than previously suspected. It is also concluded that the taxonomic authority of this species is not “Aymard, 1846”, as previously published by many authors, but “Gervais, 1850” (chapter 8). The erroneous authorship was based on a non-existent publication.
4. The taphonomic study of the large herbivore remains from the Vallparadís section (late Early Pleistocene) in NE Iberian Peninsula a clear consumption patern on long bones consistent with the activity *Pachycrocuta brevirostris* as principal bone modificator agent (chapter 7). The results support the scavenging habits previously inferred for this species in other European sites and suggest a putative competition for carcasses with early human populations of Europe.
5. The study of the internal cranial morphology of *Pliocrocuta perrieri* (chapter 9) indicates a complete development of the frontal sinuses, which has been related to increased resistance to the stresses generated in the bone-crushing bite. Coupled with other features, the development of the frontal sinuses supports a durophagous diet for

this species. It is hypothesized that such adaptation could have been later co-opted for a non-durophagous (more hypercarnivorous) diet in more derived hyaenids such as *Chasmaporthetes.*

6. The presence of a zig-zag enamel microstructural pattern is reported for *Hyaenictis* aff. *almerai* (chapter 4) and *Pliocrocuta perrieri* (chapter 5), being indicative of a durophagous diet. On this basis, *Hyaenictis* is reclassified as a transitional bone-cracking hyena (ecomorphotype 5), instead of a hunting hyena (ecomorphotype 4) as previously thought. *Hyaenictis* is supported as one of the oldest and most primitive bone-cracking hyenas, suggesting that durophagy might have independently evolved among hyaenids more times than previously suspected.
7. The study of the endocast morphology of *Pliocrocuta perrieri* (chapter 9) indicates a similar encephalization to that of extant hyaenines, a brain morphology closer to that of *Parahyaena*, and a somewhat lesser development of the frontal cortex than in *Parahyaena* and *Hyaena.* The brain endocast morphology of the extinct *Crocuta spelaea* and *Crocuta ultima* (chapter 10) shows greater similarities to the extant *Crocuta crocuta*, but with a less developed anterior brain (comparable to *Hyaena* and *Parahyaena*). These results support a solitary social behavior for the three extinct hyaenid species investigated, which would have been less gregarious than extant *Crocuta* and more similar in this regard to *Hyaena* and *Parahyaena*.
8. Currently available paleoneurological data indicate that the hyaenid brain evolved towards greater relative size and complexity throughout the Miocene (chapter 11), with the condition of *Proteles* being the most plesiomorphic among extant hyaenids, given its similarities with that of the Miocene *Adcrocuta* (appendix). The enlargement of the frontal cortex played a most prominent role in the evolution of more complex behaviors (chapters 9 and 10), as best shown by the autapomorphic condition of extant *Crocuta crocuta*.
9. The evolutionary history of hyaenids, with emphasis on bone-cracking taxa, is revisited in the light of the new data provided in this dissertation (chapter 11). Given some discrepancies between currently favored phylogenetic hypotheses and both fossil and molecular evidence, some alternate hypotheses are proposed (e.g., a close link between *Adcrocuta* and *Thalassictis,* the origin of hyaenines from *Hyaenictis*, and a closer relationship between *Pliocrocuta* with a *Hyaena*+*Parahyaena* exclusive of *Crocuta*; chapters 5 and 9). These hypotheses should be tested in the future by rigorous cladistic analyses incorporating additional characters from internal cranial morphology—which, given their taxonomic utility (as shown *Crocuta*; chapter 10),

might hopefully contribute to a better resolution of the relationships among both extant and extinct hyaenids.

References

Adrover, R., Aguirre, E., Heintz, E., Moissenet, E., & Morales, J. (1974). Formaciones Plio-Pleistocenas del Llano de Sarrión. In: Aguirre, E., & Morales, J. (eds). Coloquio Internacional Bioestratigrafía Continental del Neógeno superior y Cuaternario inferior, Teruel II, guía, pp 3–10.

Aguirre, E., & Soto, E. (1974). Nuevo fósil de Cercopitécido en el Pleistoceno inferior de La Puebla de Valverde (Teruel). *Estudios Geológicos 30*, 213–217.

Aguirre, E., & Soto, E. (1978). *Paradolicopithecus* in La Puebla de Valverde, Spain: Cercopithecoidea in European Neogene Stratigraphy. *Journal of Human Evolution 7*, 559–565.

Agustí, J., Cabrera, L., & Moyà-Solà, S. (1985). Sinopsis estratigráfica del Neógeno de la fosa del Vallés-Penedés. *Paleontologia i Evolució 18*, 57–81.

Agustí, J., Cabrera, L., Garcés, M., & Parés, J.M. (1997). The Vallesian mammal succession in the Vallès-Penedès basin (northeast Spain): Paleomagnetic calibration and correlation with global events. *Palaeogeography, Palaeoclimatology, Palaeoecology 133*, 149–180.

Alberdi, M., Azanza, B., Cerdeño, E., & Prado, J. (1997). Similarity relationship between mammal faunas and biochronology from Latest Miocene to Pleistocene in the Western Mediterranean area. *Eclogae Geologicae Helvetiae 90*, 115–132.

Anderson, M.D., Richardson, P.R.K., & Woodall, P.F. (1992). Functional analysis of the feeding apparatus and digestive tract of the aardwolf *Proteles cristatus*. *Journal of Zoology 228*, 423–434.

Andersson, K. (2005). Were there pack-hunting canids in the Tertiary, and how can we know?. *Paleobiology 31*, 56–72.

Andersson, K., & Werdelin, L. (2005). Carnivora from the Late Miocene of Lantian, China. *Vertebrata PalAsiatica 43*, 256–271.

Andrés Rodrigo, M. (2011). Los bóvidos villafranquienses de La Puebla de Valverde y Villarroya: Sistemática, filogenia y Paleobiología. Unpublished Ph.D. Dissertation, Universidad de Zaragoza.

Andrés, M., Azanza, B., & Morales, J. (2016). Artiodáctilos del yacimiento villafranquiense de Villarroya. In: Alberdi, M.T., Azanza, B., & Cervantes, E., (eds). Villarroya, yacimiento clave de la paleontología riojana. Instituto de estudios Riojanos, Logroño, pp 159–176.

Antón, M., Galobart, A., & Turner, A. (2005). Co-existence of scimitar-toothed cats, lions and hominins in the European Pleistocene. Implications of the post-cranial anatomy of *Homotherium latidens* (Owen) for comparative palaeoecology. *Quaternary Science Reviews 24*, 1287–1301.

Antón, M., Turner, A., Salesa, M.J., & Morales, J. (2006). A complete skull of *Chasmaporthetes lunensis* (Carnivora, Hyaenidae) from the Spanish Pliocene site of La Puebla de Valverde (Teruel). *Estudios Geológicos 62*, 375–388.

Apps, P.J., Viljoen, H.W., Richardson, P.R.K., & Pretorius, V. (1989). Volatile components of anal gland secretion of the aardwolf (*Proteles cristatus*). *Journal of Chemical Ecology 15*, 1681–1688.

Arribas, A., & Palmqvist, P. (1998). Taphonomy and palaeoecology of an assemblage of large mammals: hyaenid activity in the lower Pleistocene site at Venta Micena (Orce, Guadix-Baza Basin, Granada, Spain). *Geobios 31*, 3–47.

Arsznov B.M., Lundrigan, B.L., Holekamp, K.E., & Sakai, C.T. (2010). Sex and the Frontal Cortex: A Developmental CT Study in the Spotted Hyena. *Brain, Behavior and Evolution* 77, 91–104.

Bakr, A. (1959). Rodentia and Carnivora from the Pontian of Samos. Ph.D. Dissertation, Harvard University.

Barton, R.A., & Dunbar, R.I.M. (1997). Evolution of the social brain. In: Whiten, A., Byrne, R. (eds). Machiavellian Inteligence II. Cambridge Unversity Press, Cambridge, pp 240–263.

Bartrina, M.T., Cabrera, L., Jurado, M.J., Guimerà, J., & Roca, E. (1992). Evolution of the central Catalan margin of the Valencia trough (western Mediterranean). *Tectonophysics 203*, 219–247.

Baryshnikov, G. (1999). Chronological and geographical variability of *Crocuta spelaea* (Carnivora, Hyaenidae) from the Pleistocene of Russia. *Deinsea 6*, 155–174.

Baryshnikov, G., & Tsoukala, E. (2010). New analysis of the Pleistocene carnivores from Petralona Cave (Macedonia, Greece) based on the Collection of the Thessaloniki Aristotle University. *Geobios 43*, 389–402.

Bearder, S.K. (1977). Feeding habits of spotted hyaenas in a woodland habitat. *African Journal of Ecology 15*, 263–280.

Bearder, S.K., & Randall, R.M. (1978). The use of fecal marking sites by hyaenas and civets. *Carnivore 1*, 32–48.

Bennett, E.T. (1833). Notice of a new genus of Viverridous Mammalia from Madagascar. *Proceedings of the Zoological Society of London 1833*, 46.

Berástegui, X., Casanovas J. & Moyà-Solà S. (2000): El jaciment paleontològic de Cal Guardiola. Una finestra oberta al Plistocè inferior de Catalunya. Contextualització geològica. *Tribuna d'Arqueologia 1997-1998*, 255–277.

Beràstegui, X., & Losantos, M. (2001). Mapa geològic, Full 392-2-2, Sabadell. ICGC, Barcelona.

Bernor, R.L. (1983). Geochronology and zoogeographic relationships of Miocene Hominoidae. In: Ciochon, R.L., & Corruccini, R.S. (eds). New Interpretations of Ape and Humen Ancestry. Plenum Press, New York, pp 21–64.

Bernor, R.L. (1984). A zoogeographic theater and biochronologic play: Time/biofacies phenomena of Eurasian and African Miocene mammal province. *Paléogiologie Continentale 14*, 121–142.

Berta, A. (1981). The Plio-Pleistocene hyaena *Chasmaporthetes ossifragus* from Florida. *Journal of Vertebrate Paleontology 1*, 341–356.

Bertram, B.C.R. (1979). Serengeti predators and their social systems. In: Sinclair, A.R.E., & Norton-Griffiths, M. (eds). Serengeti, dynamics of an ecosystem. University of Chicago Press, Chicago, pp 221–248.

Bininda-Emonds, O.R., Gittleman, J.L., & Purvis, A. (1999). Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biological Reviews of the Cambridge Philosophical Society 74*, 143–175.

Blaya Martí, E., Obradó, P., Robles, J.M., Sala, J., & Alba, D.M. (2012). Memòria de la intervenció paleontològica preventiva a les obres de prolongació de la Ronda Oest Sabadell tram comprès entre la carretera N-150 i la BV-1248 (Sabadell, el Vallès Occidental): 2008–2011. FOSSILIA Serveis Paleontològics i Geològics SL (unpublished report).

Boaz, N.T., Ciochon, R.L., Xu, Q., & Liu, J. (2000). Large Mammalian Carnivores as a Taphonomic Factor in the Bone Accumulation at Zhoukoudian. *Acta Anthropologica Sinica 19 supplementary*, 224–234.

Bologna, P., Di Stefano, G., Manzi, G., Petronio, C., Sardella, R., & Squazzini, E. (1994). Late Pleistocene mammals from the Melpignano (LE) "Ventarole": preliminary analysis and correlations. *Bollettino della Società Paleontologica Italiana 33*, 265–274.

Borissiak, A. (1915). Mammiferes Fossiles de Sebastopol, II. *Mèmoires du Comité Géologique, Petrograd 137*, 1–47.

Bothma, J.D.P. (1971). Food habits of some Carnivora (Mammalia) from southern Africa. *Annals of the Transvaal Museum 27*, 15–26.

Bothma, J.D.P. (1998). Carnivore ecology in arid lands. 212 pp. Springer Verlag, Berlin.

Bothma, J.D.P., & Nel, J.A.J. (1980). Winter food and foraging behaviour of the aardwolf *Proteles cristatus* in the Namib-Naukluft Park. *Madoqua 12*, 141–149.

Bothma, J.D.P., & Walker, C. (2013). Larger carnivores of the African savannas. 274 pp. Springer Science & Business Media, Pretoria.

Bothma, J.D.P., Nel, J.A.J., & Macdonald, A. (1984). Food niche separation between four sympatric Namib Desert carnivores. *Journal of Zoology 202*, 327–340.

Bouskila, Y. (1984). The foraging groups of the striped hyaena (*Hyaena hyaena syriaca*). *Carnivore 7*, 2–12.

Bowdich, T. E. (1821). An analysis of the natural classifications of Mammalia: for the use of students and travelers. 115 pp. J. Smith, Paris.

Brisson, M.J. (1762). Regnum animale in classes IX distributum, sive synopsis methodica sistens classium, quadripedum scilicet & cetaceorum, particularum divisionem in ordines, sectiones, genera & species. Editio altera auctior (2nd ed.). 296 pp. Theodorum Haak, Leiden.

Broom, R., & Schepers, G.W.H. (1946). The South African fossil ape-men. The Australopithecinae. *Transvaal Museum Memoires 2*, 1–272.

Burgener, N., & Gusset, M. (2003). The feeding habits of brown hyaenas (*Hyaena brunnea*) on a game ranch in Limpopo Province, South Africa. *African Zoology 38*, 181–184.

Burgener, N., Dehnhard, M., Hofer, H., & East, M.L. (2009). Does anal gland scent signal identity in the spotted hyaena? *Animal Behaviour 77*, 707–715.

Burgener, N., East, M.L., Hofer, H., & Dehnhard, M. (2008). Do spotted hyena scent marks code for clan membership?. In: Hurst, J.L., Benyon, R.J., Roberts, S.C. & Wyatt, T.D. (eds). Chemical Signals in Vertebrates XI. Springer, New York, pp 169–177.

Byrne, R., & Whiten, A. (1988). Machiavellian Intelligence. 430 pp. Oxford University Press, Oxford

Cabrera, L. (1981). Influencia de la tectónica en la sedimentación continental de la cunenca del Vallès-Penedès (provincia de Barcelona, España) durante el Mioceno inferior. *Acta geológica hispánica 16*, 163–169.

Cabrera, l., & Calvet, F. (1990). Sequential arrangement of the Neogene sedimentary record in the Vallès-Penedès and Valls-Reus half grabens. Iberian margins, NE Spain. *Terra Abstracts 2*, 1–110.

Cabrera, L., & Calvet, F. (1996). Onshore Neogene record in NE Spain: Vallès-Penedès and El Camp half-grabens (NW Mediterranean). In: Friend, P.F., & Dabrio, C.J. (eds). Tertiary Basins of Spain. Cambridge University Press, Cambridge, pp 97–105.

Cabrera, L., Roca, E., Garcés, M. & de Porta, J. (2004). Estratigrafía y evolución tectonosedimentaria oligocena superior-neógena del sector central del margen catalán (Cadena Costero-Catalana). In: Vera, J.A. (ed). Geología de España. SGE-IGME, Madrid, pp 569–573.

Carbonell, E., Estevez, J., Moyà-Solà, S., Pons-Moyà, J., Agustí, J., & Villalta, J.F. (1981). «Cueva Victoria» (Murcia, España): Lugar de ocupación humana más antiguo de la Península Ibérica. *Endins 8*, 47–57.

Carvajal, E. (1926). Nota sobre un yacimiento de fósiles de vertebrados en el Plioceno de la provincia de Logroño. *Boletín del Instituto Geologico de España 47*, 317–333.

Casanovas-Vilar, I., Alba, D.M., Moyà-Solà, S., Galindo, J., Cabrera, L., Garcés, M., Furió M., Robles, J.M., Köhler, M., & Angelone, C. (2008). Biochronological, taphonomical, and paleoenvironmental background of the fossil great ape *Pierolapithecus catalaunicus* (Primates, Hominidae). *Journal of Human Evolution 55*, 589–603.

Casanovas-Vilar, I., Alba, D., Robles, J., & Moyà-Solà, S. (2011). Registro paleontológico continental del Mioceno de la cuenca del Vallès-Penedès. *Paleontologia i Evolució, Memòria especial 6*, 55–80.

Casanovas-Vilar, I., Almécija, S., & Alba, D.M. (2015). Late Miocene flying squirrels from Can Llobateres 1 (Vallès-Penedès Basin, Catalonia): systematics and palaeobiogeography. *Palaeobiodiversity and Palaeoenvironments 95*, 353–372.

Casanovas-Vilar, I., Angelone, C., Alba, D.M., Moyà-Solà, S., Köhler, M., & Galindo, J. (2010). Rodents and lagomorphs from the Middle Miocene hominoid-bearing site of Barranc de Can Vila 1 (els Hostalets de Pierola, Catalonia, Spain). *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen 257*, 297–315.

Casanovas-Vilar, I., Madern, A., Alba, D.M., Cabrera, L., García-Paredes, I., van den Hoek Ostende, L., DeMiguel, D., Robles, J.M., Furió, M., van Dam, J., Garcés, M., Angelone, C., & Moyà-Solà, S. (2016a) The Miocene mammal record of the Vallès-Penedès Basin (Catalonia). *Comptes Rendus Palevol 15*, 791–812.

Casanovas-Vilar, I., Crespo, M.G., Van Dam, J., García-Paredes, I., Robles, J.M., & Alba, D.M. (2016b). An updated biostratigraphy for the late Aragonian and Vallesian of the Vallès-Penedès Basin (Catalonia). *Geologica Acta 14*, 195–217.

Cerdeño, E., & Alberdi, M.T. (2016). Los Perisodáctilos de Villarroya. In: Alberdi, M.T., Azanza, B., & Cervantes, E., (eds). Villarroya, yacimiento clave de la paleontología riojana. Insituto de Estudios Riojanos, Logroño, pp 143–158.

Child, G., & Robbel, H. (1975). Drowning of lechwe by spotted hyaena. *Mammalia 39*, 705.

Colbert, E.H. (1939). Carnivora of the Tung Gur Formation of Mongolia. *Bulletin of the American Museum of Natural History 76*, 47–81.

Cooper, S.M. (1990a). The hunting behaviour of spotted hyaenas (*Crocuta crocuta*) in a region containing both sedentary and migratory populations of herbivores. *African Journal of Ecology 28*, 131–141.

Cooper, S.M. (1990b). Clan sizes of spotted hyaenas in the Savuti region of the Chobe National Park, Botswana. *Botswana Notes and Records 21*, 121–133.

Cooper, S.M. (1991). Optimal hunting group size: the need for lions to defend their kills against loss to spotted hyaenas. *African Journal of Ecology 29*, 130–136.

Cooper, S.M. (1993). Denning behaviour of spotted hyaenas (*Crocuta crocuta*) in Botswana. *African Journal of Ecology 31*, 178–180.

Cooper, S.M., Holekamp, K.E., & Smale, L. (1999). A seasonal feast: long-term analysis of feeding behaviour in the spotted hyaena (*Crocuta crocuta*). *African Journal of Ecology 37*, 149–160.

Cope, E.D. (1892). A hyaena and other Carnivora from Texas. *Proceedings of the Natural Academy of Sciences U.S.A. 44*, 326–327.

Croizet, J.B. & Jobert, A.C.G. (1828). Recherches sur les Ossements Fossiles du Département du Puy-de-Dôme. 224 pp. Delahays, Paris.

Crusafont Pairó, M. (1952). Los jiráfidos fósiles de España. *Memorias y Comunicaciones del Instituto Geológico 8*, 1–239.

Crusafont Pairó, M., & Aguirre, E. (1972). *Stenailurus*, Félidé nouveau, du Turolien d'Espagne. *Annales de Paléontologie 58*, 211–223.

Crusafont Pairó, M., & Petter, G. (1969). Contribution à l'étude des Hyaenidae. La sous-famille des Ictitheriinae. *Annales de Paléontologie (Vertébrés) 55*, 89–127.

Crusafont, M., Hartenberger, J., & Heintz, E. (1964). Un nouveau gisement de Mammiféres fossiles d'áge Villafranchien a la Puebla de Valverde (Province de Teruel, Espagne*). Comptes Rendus de l'Academie de Sciences de Paris 258*, 2869–2871.

David, A. (1869). Etrait d'une lettre du meme, dateé de la Principaute Thibetaine (independente) de Mou-pin, le 21 Mars 1869. *Nouvelles Archives du Muséum d'Histoire Naturelle, Paris 5*, 12–13.

Davidar, E.R.C. (1990). Observation at a hyena *Hyaena hyaena* den. *Journal of the Bombay Natural History Society 87*, 445–447.

Davis, D.D. (1964). The giant panda: a morphological study of evolutionary mechanism. *Fieldiana Zoolology Memoirs 3*, 1–339.

de Beaumont, G. (1964). Note sur le región otique d'*Ictitherium hipparionum* (Gervais) (Carnivora). *Archives des Sciences 17*, 339–342.

de Beaumont, G. (1967). Observations sur les Herpestinae (Viverridae, Carnivora) de l'Oligocène supérieur avec quelques remarques sur les Hyaenidae du Néogène. *Archives des Sciences 20*, 79–108.

de Beaumont, G. (1968). Une intéressante mandibule de Hyaenidae (Carnivora) du Pontien de Samos. *Archives des Sciences 22*, 21–26.

de Beaumont, G. (1969a). Breves remarques a propos d'un crane de Hyaenidae (Carnivora) du Musee de Vienne. *Archives des Sciences 22*, 49–54.

de Beaumont, G. (1969b). Breves remarques sur *Plioviverrops* Kretzoi (Carnivora). *Bulletin de la Societe Vaudoise des Sciences Naturelles 70*, 1–7.

de Beaumont, G., & Mein, P. (1972). Recherces sur le genre *Plioviverrops* Kretzoi (Carnivora, Hyaenidae). *Archives des Sciences 25*, 383–394.

de Blainville, H.M.D. (1842). Ostéographie ou description iconographique compare dus squelette et du système dentaire des Mammifères récents et fossils pour server de base à la zoologie et à la géologie 2. 152 pp. J.B. Bailière et Fils, Paris.

de Blainville, H.M.D. (1844). Osteographie, ou description iconographique comparee du squelette et du systeme dentaires des Mammiferes recent et fossiles. 66 pp. J.B. Bailière et Fils, Paris.

de Bonis, L. (2004). Carnivores hyaenidés du Miocène supérieur de Turquie. *Zona Arquaeologica, Miscelanea en homenaje a Emiliano Aguirre 2*, 108–117.

de Bonis, L. (2005). Carnivora (Mammalia) from the late Miocene of Akkas¸dag˘ ı, Turkey. *Geodiversitas 27*, 567–589.

de Bonis, L., & Koufos, G.D. (1981). A New Hyaenid (Carnivora, Mammalia) in the Vallesian (Late Miocene) of Northern Greece. *Science Annals, Faculty of Physics & Mathematics, University of Thessaloniki 21*, 79–94.

de Bonis, L., & Koufos, G.D. (1994). Some hyaenids from the late Miocene of Macedonia (Greece) and the Phylogeny of hunting hyenas. *Münchner geowissenschaftliche Abhandlungen 26*, 81–96.

de Bonis, L., Peigné, S., Likius, A., Mackaye, H.T., Vignaud, P., & Brunet, M. (2005). *Hyaenictitherium minimum*, a new ictithere (Mammalia, Carnivora, Hyaenidae) from the late Miocene of Toros-Menalla, Chad. *Comptes Rendus Palevol 4*, 671–679.

de Gibert, J.M., & Casanovas-Vilar, I. (2011). Contexto geológico del Mioceno de la cuenca del Vallès-Penedès. *Paleontologia i Evolució, memòria especial 6*, 39–45.

Deane, N.N. (1962). The spotted hyaena *Crocuta crocuta*. *Lammergeyer 2*, 26–44.

Del Campana, D. (1914). La *Lycyaena lunensis* n. sp. dell'ossario pliocenico di Olivola (Val di Magra). *Paleontographia Italica 20*, 87–104.

Dennell, R.W., Coard, R., & Turner, A. (2008). Predators and scavengers in Early Pleistocene southern Asia. *Quaternary International 192*, 78–88.

Depéret, D.J. (1892). La faune des mammifères miocènes de La Grive St-Alban. *Archives du Museum, Lyon 5*, 1–89.

Diedrich, C.G. (2006). The *Crocuta crocuta spelaea* (Goldfuss 1823) population from the early Late Pleistocene hyena open air prey deposit site Biedensteg (Bad Wildungen, Hess, NW Germany), a contribution to their phylogenetic position, coprolites and prey. C*ranium 23*, 39–53.

Diedrich, C.G. (2007). The Upper Pleistocene *Crocuta crocuta spelaea* (Goldfuss 1823) population and its prey from the gypsum karst den site Westeregeln near Magdeburg (Middle Germany). *Abhandlungen und Berichte für Naturkunde Magdeburg 30*, 57–83.

Diedrich, C.G. (2011). A clan of Late Pleistocene hyenas, *Crocuta crocuta spelaea* (Goldfuss 1823), from the Rösenbeck Cave (Germany) and a contribution to cranial shape variability. *Biological Journal of the Linnean Society 103*, 191–220.

Dong, W. (2008). Virtual cranial endocast of the oldest giant panda (*Ailuropoda microta*) reveals great similarity to that of its extant relative. *Naturwissenschaften 95*, 1079–1083.

Dunbar, R.I.M. (1998). The social brain hypothesis. *Evolutionary Anthropology 6*, 178–190.

Dunbar, R.I.M., & Shultz, S. (2007). Evolution in the social brain. *Science 317*, 1344–1347.

East, M.L., & Hofer, H. (1991a). Loud calling in a female-dominated mammalian society: I. Structure and composition of whooping bouts of spotted hyaenas, *Crocuta crocuta*. *Animal Behaviour 42*, 637–649.

East, M.L., & Hofer, H. (1991b). Loud calling in a female-dominated mammalian society: II. Behavioural contexts and functions of whooping of spotted hyaenas, *Crocuta crocuta*. *Animal Behaviour 42*, 651–669.

East, M.L., & Hofer, H. (2001). Male spotted hyenas (*Crocuta crocuta*) queue for status in social groups dominated by females. *Behavioral Ecology 12*, 558–568.

East, M.L., Hofer, H., & Turk, A. (1989). Functions of birth dens in spotted hyaenas. *Journal of Zoology, London 219*, 690–697.

East, M.L., Hofer, H., & Wickler, W. (1993). The erect 'penis' is a flag of submission in a female-dominated society: greetings in Serengeti spotted hyenas. *Behavioral Ecology and Sociobiology 33*, 355–370.

East, M.L., Burke, T., Wilhelm, K., Greig, C., & Hofer, H. (2003). Sexual conflicts in spotted hyenas: male and female mating tactics and their reproductive outcome with respect to age, social status and tenure. *Proceedings of the Royal Society of London B 270*, 1247–1254.

Eaton, R.L. (1976). The brown hyaena: a review of biology, status and conservation. *Mammalia 40*, 377–399.

Eloff, F.C. (1964). On the predatory habits of lions and hyaenas. *Koedoe 7*, 105–112.

Eloff, F.C. (1984). Food ecology of the Kalahari lion *Panthera leovernayi*. *Koedoe 27*, 249–258.

Erxleben, J.C.P. (1777). Systema regni animalis, Classis I, Mammalia. 636 pp. Impensis Weygandianis, Leipzig.

Espigares, M.P. (2010). Análisis y Modelización del Contexto Sedimentario y los Atributos Tafonómicos de los Yacimientos Pleistocénicos del borde Nororiental de la Cuenca de Guadix-Baza. Ph.D. Dissertation, Universidad de Granada.

Evans, H.E. (1993). Miller's Anatomy of the Dog. Third Edition. 1130 pp. Saunders, Philadelphia.

Evans, H.E., & De Lahunta, A. (2013). Miller's Anatomy of the Dog. Fourth edition. 872 pp. Elsevier Health Sciences.

Ewer, R. (1955). The fossil carnivores of the Transvaal caves. The lycyaenas of Sterkfontein and Swartkrans, together with some general considerations of the Transvaal fossil hyaenids. *Proceedings of the Zoological Society of London 124*, 839–857.

Ewer, R.F. (1973). The carnivores. 494 pp. Cornell University Press, Ithaca.

Falconer, H. (1867). Fauna Antiqua Siwalensis, Volume 1. 590 pp. Robert Hardwicke, London.

Fernández de Bobadilla, F. (1963a). El yacimiento de mamíferos fósiles de Villarroya. *Berceo 67*, 211–217.

Fernández de Bobadilla, F. (1963b). El yacimiento de mamíferos fósiles de Villarroya. *Berceo 69*, 387–393.

Fernández de Bobadilla, F. (1964a). El yacimiento de mamíferos fósiles de Villarroya. *Berceo 70*, 29–54.

Fernández de Bobadilla, F. (1964b). El yacimiento de mamíferos fósiles de Villarroya. *Berceo 72*, 257–272.

Ferrández-Cañadell, C. (2015). Contexto sedimentario y tafonomia de Cueva Victoria. *Mastia 11–13,* 139–162.

Ferrández-Cañadell, C., & Gibert, L. (2015). Introducción. Cueva Victoria, un yacimiento de vertebrados del Pleistoceno Inferior. *Mastia 11–13*, 17–45.

Ferretti, M.P. (1999). Tooth enamel structure in the hyaenid *Chasmaporthetes lunensis* lunensis from the late Pliocene of Italy, with implications for feeding behavior. *Journal of Vertebrate Paleontology 19*, 767–770.

Ferretti, M.P. (2007). Evolution of bone-cracking adaptions in hyaenids (Mammalia, Carnivora). *Swiss Jourrnal of Geosciences 100*, 41–52.

Ficcarelli, G., & Torre, D. (1970). Remarks on the taxonomy of hyaenids. *Palaeontographia Italica 66*, 13–33.

Figueirido, B., Serrano-Alarcón, F.J., & Palmqvist, P. (2012). Geometric morphometrics shows differences and similarities in skull shape between the red and giant pandas. *Journal of Zoology 286*, 293–302.

Figueirido, B., Serrano-Alarcón, F.J., Slater, G.J., & Palmqvist, P. (2010). Shape at the cross-roads: homoplasy and history in the evolution of the carnivoran skull towards herbivory. *Journal of Evolutionary Biology 23,* 2579–2594.

Figueirido, B., Tseng, Z.J., & Martín-Serra, A. (2013). Skull shape evolution in durophagous carnivorans. *Evolution 67*, 975-993.

Finarelli, J.A. (2008). Testing hypotheses of the evolution of brain-body size scaling in the Canidae (Carnivora, Mammalia). *Paleobiology 34*, 35–45.

Finarelli, J.A., & Flynn, J.J. (2007). The evolution of encephalization in caniform carnivorans. *Evolution 61*, 1758–1772.

Finarelli, J.A., & Flynn, J.J. (2009). Brain-size evolution and sociality in Carnivora. *Proceedings of the National Academy of Sciences USA 106,* 9345–9349.

Flower, S. (1932). Notes on the recent mammals of Egypt, with a list of the species recorded from that Kingdom. *Proceedings of the Zoological Society of London 1932*, 369–450.

Flower, W.H. (1869). On the value of the characters of the base of the cranium in the classification of the order Carnivora and on the systematic position of Bassaris and other disputed forms. *Proceedings of the Royal Society London 1869*, 4–37.

Flynn, J.J. & Galiano, H. (1982). Phylogeny of early Tertiary Carnivora, with a description of a new species of *Protictis* from the Middle Eocene of Northwestern Wyoming. *American Museum Novitates 2725*, 1–64.

Flynn, J.J., & Nedbal, M.A. (1998). Phylogeny of the Carnivora (Mammalia): congruence vs incompatibility among multiple data sets. *Molecular Phylogenetics and Evolution 9*, 414–426.

Flynn, J.J., Finarelli, J.A., Zehr, S., Hsu, J. & Nedbal, M.A. (2005). Molecular Phylogeny of the Carnivora (Mammalia): Assessing the Impact of Increased Sampling on Resolving Enigmatic Relationships. *Systematic Biology 54*, 317–337.

Flynn, J.J., Nedbal, M.A., Dragoo, J.W. & Honeycutt, R.L. (2000). Whence the Red Panda?. *Molecular Phylogenetics and Evolution 17*, 190–199.

Flynn, J.J., Neff, N.A. & Tedford, R. H. (1988). Phylogeny of the Carnivora. In: Benton, M.J. (ed). The phylogeny and classification of the tetrapods. Clarendon Press, Oxford, pp 73–115.

Forsyth Major, C.I. (1903). New Carnivora from the middle Miocene of La Grive St-Alban. *Geological Magazine 1*, 534–538.

Fraile, S. (2015). Estudio de *Protictitherium crassum* del Cerro de los Batallones (Torrejón de Velasco, Madrid): aportación a la filogenia y evolución de la familia Hyaenidae. Ph.D. Dissertation, Universidad Complutense de Madrid.

Frank, L.G. (1986a). Social organization of the spotted hyaena (*Crocuta crocuta*). II. Dominance and reproduction. *Animal Behavior 34*, 1510–1527.

Frank, L.G. (1986b). Social organization of the spotted hyaena (*Crocuta crocuta*). I. Demography. *Animal Behavior 34,* 1500–1509.

Frank, L.G., Holekamp, K.E., & Smale, L. (1995). Dominance, demography, and reproductive success of female spotted hyaenas. In: Sinclair, A.R.E., & Arcese, P. (eds). Serengeti II: dynamics, management and conservation of an ecosystem. University of Chicago Press, Chicago, pp 364–384.

Galiano, H., & Frailey, D. (1977). *Chasmaporthetes kani*, New species from China, with remarks on phylogenetic relationships of genera within the Hyaenidae (Mammalia, Carnivora). *American Museum Novitates 2636*, 1–16.

Galobart, A., Antón, M. & Maroto, J. (2003). Hiénidos y cánidos de los yacimientos de Incarcal (Girona, NE de la Península Ibérica): una aproximación a la paleobiología del hiénido del Pleistoceno inferior. *Paleontologia i evolució 34*, 79–98.

García Fernández, D., & Cerdeño, E. (1989). Nuevos datos sobre *Aceratherium incisivum* (Rhinocerontidae) del Turoliense de Piera (Barcelona) y Concud (Teruel). *Bulletí del Centre d'Estudis de la Natura del Barcelonès Nord 4*, 279–289.

García, N. (2003). Osos y otros carnívoros de la Sierra de Atapuerca. Unpublished Ph.D. dissertation, Fundación Oso de Asturias.

García, N., & Arsuaga, J.L. (1999). Carnivores from the Early Pleistocene hominid-bearing Trinchera Dolina 6 (Sierra de Atapuerca, Spain). *Journal of Human Evolution 37*, 415–430.

García, N., & Arsuaga, J.L. (2001). Les carnivores (Mammalia) des sites du Pléistocène ancien et moyen d'Atapuerca (Espagne). *L'Anthropologie 105*, 83–93

Gasaway, W.C., Mossestad, K.T., & Stander, P.E. (1991). Food acquisition by spotted hyaenas in Etosha National Park, Namibia: predation versus scavenging. *African Journal of Ecology 29*, 64–75.

Gaubert, P., & Veron, G. (2003). Exhaustive sample set among Viverridae reveals the sister-group of felids: the linsangs as a case of extreme morphological convergence within Feliformia. *Proceedings of the Royal Society of London B 270*, 2523–2530.

Gaudry, A. (1861). Note sur les carnassiers fossiles de Pikermi (Grèce). *Bulletin de la Société Géologique de France 18,* 527–537.

Gaudry, A. (1862-1867). Animaux fossiles et géologie de l'Attique. 475 pp. F. Savy, Paris.

Gaudry, A. (1873). Animaux fossils du Mont Léberon. 180 pp. F. Savy, Paris.

Gaudry, A., & Lartet, E. (1856). Résultats des rechercches paleontologiques dans l'Attique sous les auspices de l'Academie. *Comptes Rendus de l'Academie des Sciences, Paris 43*, 271–274, 318–321.

Gautier, F., & Heintz, E. (1974). Le gisement villafranchien de La Puebla de Valverde (Province de Teruel, Espagne). *Bulletin du Muséum National d'Histoire Naturelle, 228*, 113–136.

Geoffroy Saint-Hilaire, I. (1824). Description d'un noveau genre de mammifères carnassiers sous le nom de Protèle. *Mémoires du Muséum d'Histoire Naturelle, Paris 11*, 354–371.

Geoffroy Saint-Hilaire, I. (1851). Catalogue méthodique de la collection des mammiferes. 96 pp. Muséum d'Histoire Naturelle, Paris.

Gervais, P. (1846). Observations sur diverses espèces de mamifères fossils du midi de France. *Annales des Sciences Naturelles 5*, 248–265.

Gervais, P. (1850). Zoologie et Paléontologie Françaises. 136 pp. Arthur Bertrand, Paris.

Gervais, P. (1859). Zoologie et Paléontologie Françaises. 344 pp. Arthur Bertrand, Paris.

Gibert, J., Campillo, D., Martínez, B., Ribot, F., Caporicci, R., & Ferrández, C. (1993). Nuevos restos humanos en los yacimientos del Pleistoceno inferior de Orce y Cueva Victoria. In: Aleixandre, T., & Pérez González, A. (eds). El Cuaternario en España y Portugal, vol. 1. Instituto Tecnologico y Geominero de España, Madrid.

Gibert, J., Sánchez, F., Malgosa, A., Walker, M.J., Palmqvist, P., Martínez, B., Ribot, F. (1992). Nuevos descubrimientos de restos humanos en los yacimientos de Orce y Cueva Victoria. In: Gibert, J. (ed). Presencia humana en el Pleistoceno inferior de Granada y Murcia. Museo de Prehistoria y Paleontología J. Gibert, Orce, pp 391–414.

Gibert, L., & Scott, G. (2015). Edad del yacimiento de Cueva Victoria y su relación con otros yacimientos de la Peninsula Ibérica. *Mastia 12,* 85–100.

Ginsburg, L., & Bulot, C. (1982). Les carnivores du miocènee de Bezian près de Romieu (Gers, France). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B 85*, 53–76.

Gittleman, J.L. (1994). Are the pandas successful specialists or evolutionary failures? *BioScience 44*, 456-464.

Goldfuss, A. (1823). Osteologische Beiträgezur Kenntnis verschiedener Säugthiere de Vorwelt. *Nova Acta Physico-Medica Academiae Cesareae Leopoldino-Carolinae 21*, 449–490.

Gorman, M.L., & Mills, M.G.L. (1984). Scent-marking strategies in hyaenas (Mammalia). *Journal of Zoology 202*, 535–547.

Gray, J.E. (1821). On the natural arrangement of vertebrose animals. *London Medical Reposository 15*, 296–310.

Gregory, W. K., & Hellman, M. (1939). On the evolution and major classification of the civets (Viverridae) and allied fossil and recent Carnivora: a phylogenetic study of the skull and dentition. *Proceedings of the American Philosophical Society 81*, 309–392.

Guanfang, C., & Schmidt-Kittler, N. (1983). The deciduous dentition of *Percrocuta* Kretzoi and the diphyletic origin of hyaenas (Carnivora, Mammalia). *Paläontologische Zeitschrift 57*, 159–169.

Haile-Selassie, Y., & Howell, F.C. (2009). Carnivora. In: Haile-Selassie, Y., & Wolde Gabriel, G. (eds). *Ardipithecus kadabba*: Late Miocene Evidence from the Middle Awash, Ethiopia. University of California Press, Berkeley, pp 237–275.

Harrison, D.L. (1968). The Mammals of Arabia Volume II: Carnivora, Artiodactyla, Hyracoidea. 381 pp. Ernest Benn Ltd., London.

Hay, O.P. (1921). Descriptions of species of Pleistocene Vertebrata, types of specimens of most of which are preserved in the United States National Museum. *Proceedings of the United States National Museum 59*, 599–642.

Hayward, M.W. (2006). Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*). *Journal of Zoology 270*, 606–614.

Heintz, E. (1970). Les Cervidés villafranchiens de France et d'Espagne. *Mémoires du Muséum National d'Histoire Naturelle 22*, 1–303.

Heintz, E. (1978). La faune villafranchienne de La Puebla de Valverde, Teruel, Espagne. Composition qualitative et quantitative. *Géologie Méditerranéenne 5*, 277–280.

Heintz, E., & Aguirre, E. (1976). Le bois de *Croizetocerus ramosus pueblensis*, Cervidé de la faune villafranchienne de La Puebla de Valverde, Teruel (Espagne). *Estudios Geologicos 32*, 569–572.

Heintz, E., Delson, E., & Crusafont Pairó, M. (1971). Descubrimiento del género *Macaca* en el yacimiento de La Puebla de Valverde (Teruel). *Boletín de la Real Sociedad Española de Historia Natural (Geología) 69*, 299–302.

Hendey, Q.B. (1974). The late Cenozoic Carnivora of the south-western Cape Province. *Annals of the South African Museum 63*, 1–369.

Henschel, J.R. (1986). The socio-ecology of a spotted hyaena *Crocuta crocuta* clan in the Kruger National Park. Ph.D. Dissertation, University of Pretoria, Pretoria.

Henschel, J.R., & Skinner, J.D. (1987). Social relationships and dispersal patterns in a clan of spotted hyaenas *Crocuta crocuta* in the Kruger National Park. *South African Journal of ZooIology 22*, 18–24.

Henschel, J.R., & Skinner, J.D. (1990). The diet of the spotted hyaenas *Crocuta crocuta* in the Kruger National Park. *African Journal of Ecolology 28*, 69-82.

Henschel, J.R., & Skinner, J.D. (1991). Territorial behaviour by a clan of spotted hyaenas *Crocuta crocuta*. *Ethology 88*, 223–235.

Henschel, J.R., Tilson, R., & Von Blottnitz, F. (1979). Implications of a spotted hyaena bone assemblage in the Namib Desert. *The South African Archaeological Bulletin 34*, 127–131.

Hensel, R.F. (1862). Über die Reste einiger Säugetuerarten von Pikermi in der Münchener Sammlung. Monatsberichte der Köninglichen Preufs. *Akademie der Wissenschaften zu Berlin 1862*, 560–569.

Heptner, V.G., & Sludskij, A.A. (1980). Die Säugetiere der Swojetunion. Vol III: Raubtiere (Feloidea). 936 pp. Gustav Fischer Verlag, Jena.

Hill, A. (1980). Hyaena provisioning of juvenile offspring at the den. *Mammalia 44*, 594–595.

Hofer, H., & East, M.L. (1993a). The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey I. Social organization. *Animal Behavior 46*, 547–557.

Hofer, H., & East, M.L. (1993b). The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey III. Attendance and maternal care. *Animal Behavior 46*, 575–589.

Hofer, H., & East, M.L. (1995). Population dynamics, population size, and the community system of Serengeti spotted hyaenas. In: Sinclair, A.R.E., & Arcese, P. (eds). Serengeti II: dynamics, management and conservation of an ecosystem. University of Chicago Press, Chicago, pp 332–363.

Hofer, H., & East, M.L. (1997). Skewed offspring sex ratios and sex composition of twin litters in Serengeti spotted hyaenas (*Crocuta crocuta*) are a consequence of siblicide. *Applied Animal Behaviour Science 51,* 307–316.

Hofer, H., & East, M.L. (2003). Behavioral processes and costs of co-existence in female spotted hyenas: a life history perspective. *Evolutionary Ecology 17*, 315–331.

Hofer, H., & East, M.L. (2008). Siblicide in Serengeti spotted hyenas: a long-term study of maternal input and cub survival. *Behavioral Ecology and Sociobiology 62*, 341–351.

Holekamp, K. E., Boydston, E.E., & Smale, L. (2000). Group travel in social carnivores. In: Boinski, S. & Garber, P. (eds). On the move: group travel in primates and other animals. University of Chicago Press, Chicago, pp 587–627.

Holekamp, K.E., & Kolowski, J.M. (2009). Family Hyaenidae (Hyaenas). In: Wilson, D.E., & Mittermeier, R.A. (eds). Handbook of the mammals of the world. Lynx Ediciones, Barcelona, pp 234-262.

Holekamp, K.E., & Smale, L. (1993). Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relations with other immature individuals. *Animal Behaviour 46*, 451–466.

Holekamp, K.E., & Smale, L. (1995). Rapid change in offspring sex ratios after clan fission in the spotted hyena. *The American Naturalist 145*, 261–278.

Holekamp, K.E., Boydston, E.E., Szykman, M., Graham, I., Nutt, K.J., Birch, S., Piskiel, A., & Singh, M. (1999). Vocal recognition in the spotted hyaena and its possible implications regarding the evolution of intelligence. *Animal Behaviour 58*, 383–395.

Holekamp, K.E., Cooper, S.M., Katona, C.I., Berry, N.A., Frank, L.G., & Smale, L. (1997). Patterns of association among female spotted hyenas (*Crocuta crocuta*). *Journal of Mammalogy 78*, 55–64.

Holekamp, K.E., Sakai, S.T., & Lundrigan, B.L. (2007). Social intelligence in the spotted hyena (*Crocuta crocuta*). *Philosophical Transactions of the Royal Society 362*, 523–538.

Höner, O.P., Wachter, B., East, M.L., & Hofer, H. (2002). The response of spotted hyaenas to long-term changes in prey populations: functional response and interspecific kleptoparasitism. *Journal of Animal Ecology 71*, 236–246.

Höner, O.P., Wachter, B., East, M.L., Runyoro, V.A., & Hofer, H. (2005). The effect of prey abundance and foraging tactics on the population dynamics of a social, territorial carnivore, the spotted hyena. *Oikos 108*, 544–554.

Höner, O.P., Wachter, B., Hofer, H., Wilhelm, K., Thierer, D., Trillmich, F., Burke, T., & East, M.L. (2010). The fitness of dispersing spotted hyaena sons is influenced by maternal social status. *Nature Communications 1*, 60.

Houston, D.C. (1979). The adaptations of scavengers. In: Sinclair, A.R.E., & Norton-Griffiths, M. (eds). Serengeti, dynamics of an ecosystem. University of Chicago Press, Chicago, pp 263–286.

Howell, F.C., & Petter, G. (1980). The *Pachycrocuta* and *Hyaena* lineages (Plio-Pleistocene and extant species of the Hyaenidae). Their relationships with Miocene ictitheres: *Palhyaena* and *Hyaenictitherium*. *Geobios 13*, 579–623.

Howell, F.C., & Petter, G. (1985). Comparative observations on some middle and upper Miocene hyaenids. Genera: *Percrocuta* Kretzoi, *Allohyaena* Kretzoi, *Adcrocuta* Kretzoi (Mammalia, Carnivora, Hyaenidae). *Geobios 18*, 419–476.

Hunt, R.M. (1974). Auditory bulla in Carnivora – Anatomical basis for reappraisal of carnivore evolution. *Journal of Morphology 143*, 21–75.

Hunt, R.M. (1987). Evolution of the Aeluroid Carnivora: significance of auditory structure in the nimravid cat *Dinictis*. *American Museum Novitates 2886*, 1–74.

Hunt, R.M. (1989). Evolution of the Aeluroid Carnivora: Significance of the ventral promontorial process of the petrosal, and the origin of basicranial patterns in the living families. *American Museum Novitates 2930*, 1–32.

Ilani, G. (1975). Hyenas in Israel. *Israel-Land and Nature 16*, 10–18.

International Commission on Zoological Nomenclature (ICZN) (1999). International Code of Zoological Nomenclature. Fourth Edition. 306 pp. The International Trust for Zoological Nomenclature, London.

Jardim-Messeder, D., Lambert, K., Noctor, S., Pestana, F.M., de Castro Leal, M.E., Bertelsen, M. F., Alagaili, A.N., Mohammad, O.B.; Manger, P.R. & Herculano-Houzel, S. (2017). Dogs have the most neurons, though not the largest brain: Trade-off between body mass and number of neurons in the cerebral cortex of large carnivoran species. *Frontiers in neuroanatomy 11*, 118.

Jenks, S., & Werdelin, L. (1998). Taxonomy and systematics of living hyaenas (Family Hyaenidae). In: Mills, M.G.L., & Hofer, H. (eds). Hyaenas: status survey and conservation action plan. Osprey Publishing, Gland, pp 8–17.

Jiménez, S., Martín, S., & Jiménez, E. (1999). Primeros resultados de la excavación "Villarroya 88-89" (La Rioja, España). *Stvdia Geologica Salmanticensia 35*, 41–56.

Joeckel, R.M. (1998). Unique frontal sinuses in fossil and living Hyaenidae (Mammalia, Carnivora): description and interpretation. *Journal of Vertebrate Paleontology 18*, 627–639.

Johnston, H.H. (1884). The river Congo from its mouth to Bolobo. 328 pp. Low, London.

Kahlke, R.D. (2006). Untermassfeld: a late early Pleistocene (Epivillafranchian) fossil site near Meiningen (Thuringia, Germany) and its position in the development of the European mammal fauna (Vol. 1578). 141 pp. British Archaeological Reports Ltd, London.

Kaup, J.J. (1828). Über *Hyaena*, *Uromasti*, *Basiliscus*, *Corythaeolus*, *Acontias*. *Isis 21*, 1144–1150.

Kay, R.F., Ross, C., & Williams, B.A. (1997). Anthropoid origins. *Science 275*, 797–804.

Khomenko, I.P. (1914). Meiotic fauna of the village of Taraklia in the district of Bendery: Fissipedia, Rodentia, Rhinocerontidae, Equinae, Suidae, Proboscidae. *Trudy Bessarabkoe Obshchestvo Estestvois pytatelei 5*, 1–55.

Khomenko, I.P. (1932). *Hyaena borissiaki* n.sp. from the Roussillon-fauna of Bessarabia. *Travaux de l'Institut Paléozoologique de l'Academie des Sciences de l'U.R.S.S. 1*, 81–134.

Kingdon, J., & Hoffmann, M. (2013). Mammals of Africa. Volume V: carnivores, pangolins, equids and rhinoceroses. 560 pp. Bloomsbury Publishing, London.

Knight, M.H., Jaarsveld, A.S., & Mills, M.G.L. (1992). Allo-suckling in spotted hyaenas (*Crocuta crocuta*): an example of behavioural flexibility in carnivores. *African Journal of Ecology 30*, 245–251.

Koehler, C.E., & Richardson, P.R.K. (1990). *Proteles cristatus*. *Mammalian Species 353*, 1–6.

Koepfli, K.P., Jenks, S.M., Eizirik, E., Zahirpour, T., Valkenburgh, B.V., & Wayne, R.K. (2006). Molecular systematics of the Hyaenidae: relationships of a relictual lineage resolved by a molecular supermatrix. *Molecular Phylogenetics and Evolution 38,* 603–620.

Kolowski, J.M., Katan, D., Theis, K.R., & Holekamp, K.E. (2007). Daily patterns of activity in the spotted hyena. *Journal of Mammalogy 88*, 1017–1028.

Koufos, G.D. (1987). *Chasmaporthetes bonisi*, a new hyaenid (Carnivora, Mammalia) from the late Miocene of Macedoina (Greece). *Bulletin de la Société Géologique de France 8,* 913–920.

Koufos, G.D. (2000). Revision of the late Miocene carnivores from the Axios valley, Macedonia, Greece. *Münchner geowissenschaftliche Abhandlungen 39*, 51–92.

Koufos, G.D. (2009). The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. *Beiträge zur Paläontologie 31*, 57–105.

Koufos, G.D. (2011). The Miocene carnivore assemblage of Greece. *Estudios Geológicos 67*, 291–320.

Kretzoi, M. (1938). Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtfauna. *Annales Musei Nationalis Hungarici 31*, 88–157.

Kretzoi, M. (1945). Bemerkungen über das Raubtiersystem. *Annales Musei Nationalis Hungarici 38*, 59–83.

Kretzoi, M. (1951). A Csákvári Hipparion-fauna. *Földtani Közlön 81*, 384–417.

Kretzoi, M. (1952). Die Raubtiere der Hipparionfauna von Polgárdi. *Annales Musei Nationalis Hungarici 4*, 1–42.

Kretzoi, M. (1984). Felsö pannóniai. A sümeg–gerinci fauna és faunaszakasz. *Geologica Hungarica, serie geologica 20*, 214–222.

Kruuk, H. (1966). Clan-system and feeding habits of spotted hyaenas (*Crocuta crocuta* Erxleben). *Nature 209*, 1257–1258.

Kruuk, H. (1970). Interactions between populations of spotted hyaenas (*Crocuta crocuta* Erx.) and their prey species. In: Watson, A. (ed). Animal populations in relation to their food resources. Blackwell, Oxford, pp 359–374.

Kruuk, H. (1972a). The spotted hyena. A study of predation and social behavior. 388 pp. The University of Chicago Press, Chicago.

Kruuk, H. (1972b). Surplus killing by carnivores. *Journal of Zoology, London 166*, 233–244.

Kruuk, H. (1972c). The aardwolf (*Proteles cristatus* Sparrman 1783) as predator of termites. *East African Wildlife Journal 10*, 211–227.

Kruuk, H. (1976). Feeding and social behaviour of the striped hyaena (*Hyaena vulgaris* Desmarest). *African Journal of Ecology 14,* 91–111.

Kruuk, H., & Sands, W. (1972). The aardwolf (*Proteles cristata* Sparrman) 1783 as predator of termites. *African Journal of Ecology 10*, 211–227.

Kuhn, B.F., Wiesel, I., & Skinner, J.D. (2008). Diet of brown hyaenas (*Parahyaena brunnea*) on the Namibian coast. *Transactions of the Royal Society of South Africa 63*, 150–159.

Kurtén, B. (1957). The bears and hyenas of the interglacials. *Quaternaria 4*, 69–81.

Kurtén, B. (1968). Pleistocene Mammals of Europe. 317 pp. Aldine Publishing Company, Chicago.

Kurtén, B. (1976). Fossil Carnivora from the late Tertiary of Bled Douarah and Cherichira, Tunisia. *Notes du Service géologique de Tunisie 42*, 177–214.

Kurtén, B., & Werdelin, L. (1988). A review of the genus *Chasmaporthetes* Hay, 1921 (Carnivora, Hyaenidae). *Journal of Vertebrate Paleontology 8*, 46–66.

Lam, Y.M. (1992). Variability in the behaviour of spotted hyaenas as taphonomic agents. *Journal of Archaeological Science 19*, 389–406.

Laplana, C., Muñoz, A., & Pueyo, E.L. (2016). Los micromamíferos y la datación del yacimiento de Villarroya. In: Alberdi, M.T., Azanza, B., & Cervantes, E. (eds). Villarroya, yacimiento clave de la Paleontología Riojana. Insituto de Estudios Riojanos, Logroño, pp 247–267.

Leakey, L.N., Milledge, S.A.H., Leakey, S.M., Edung, J., Haynes, P., Kiptoo, D.K., & McGeorge, A. (1999). Diet of striped hyaena in northern Kenya. *African Journal of Ecology 37*, 314–326.

Lewis, M., & Werdelin, L. (1997). Evolution and ecology of the genus *Crocuta*. *Journal of Vertebrate Paleontology 17, supplement*, 60.

Lewis, M., & Werdelin, L. (2000). The evolution of spotted hyaenas (*Crocuta). Hyaena Specialist Group Newsletter 7*, 34–36.

Linnaeus, C. (1758). Systema Naturae per regna tria naturae: Secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 824 pp. Salvii, Stockholm.

Liu, J., Wagner, J., & Chen, P. (2015). Mass mortality of a large population of the spotted hyenas (*Crocuta ultima*) at the Lingxiandong Cave, Qinhuangdao, Hebei Province: a hyena communal den with its palaeoecological and taphonomical interpretation. *Quaternary Science 35*, 607–621. (in Chinese with English summary)

Lydekker, R. (1884). Siwalik and Narbada Carnivora. *Paleontologica Indica 2,* 178–351.

Macdonald, D.W. (1978). Observations on the behaviour and ecology of the striped hyaena, *Hyaena hyaena*, in Israel. *Israel Journal of Zoology 27,* 189–198.

Macdonald, D.W. (1983). The ecology of carnivore social behaviour. *Nature 301*, 379–384.

Macdonald, D.W. (1984). The encyclopaedia of mammals. 960 pp. George Allen & Unwin, London.

Maddock, A.H. (1993). Analysis of brown hyaena (*Hyaena brunnea*) scats from the central karoo, South Africa. *Journal of Zoology 231*, 679–683.

Madurell-Malapeira, J. (2010). The Villafranchian carnivores from the North-Eastern Iberian Península and the Early-Middle Pleistocene Transition. Unpublished Ph.D. Dissertation, Univeristat Autònoma de Barcelona.

Madurell-Malapeira, J., Alba, D.M., Espigares, M.P., Vinuesa, V., Palmqvist, P., Martínez-Navarro, B. & Moyà-Solà, S. (2017). Were large carnivorans and great climatic shifts limiting factors for hominin dispersals? Evidence of the activity of *Pachycrocuta brevirostris* during the Mid-Pleistocene Revolution in the Vallparadís section (Vallès-Penedès Basin, Iberian Peninsula). *Quaternary International 431*, 42–52.

Madurell-Malapeira, J., Minwer-Barakat, R., Alba, D.M., Garcés, M., Gómez, M., Aurell-Garrido, J., Ros-Montoya, S., Moyà-Solà, S., & Berástegui, X. (2010). The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe. *Quaternary Science Reviews 29*, 3972–3982.

Madurell-Malapeira, J., Robles, J.M., Casanovas-Vilar, I., Abella, J., Obradó, P., & Alba, D.M. (2014a). The scimitar-toothed cat *Machairodus aphanistus* (Carnivora: Felidae) in the Vallès-Penedès Basin (NE Iberian Peninsula). *Comptes Rendus Palevol 13*, 569–585.

Madurell-Malapeira, J., Ros-Montoya, S., Espigares, M.P., Alba, D.M. & Aurell-Garrido, J. (2014b). Villafranchian large mammals from the Iberian Peninsula: paleobiogeography, paleoecology and dispersal events. *Journal of Iberian Geology 40*, 167–178.

Marino, L., McShea, D.W., & Uhen, M.D. (2004). Origin and evolution of large brains in toothed whales. *The Anatomical Record A 281*, 1247–1255.

Martín, R.A. (2012). *Victoriamys*, a new generic name for Chaline's vole from the Pleistocene of Western Europe. *Geobios 45*, 445–450.

Martinell, J. (1988). An overview of the marine Pliocene of NE Spain. *Géologie Méditerranéenne XV*, 227–233.

Martínez-Navarro, B., & Palmqvist, P. (1995). Presence of the African machairodont *Megantereon whitei* (Broom 1937) (Felidae, Carnivora, Mammalia) in the Lower Pleistocene site of Venta Micena (Orce, Granada, Spain), with some considerations on the origin, evolution and dispersal of the genus. *Journal of Archaeological Science 22*, 569–582.

Martínez-Navarro, B., & Palmqvist, P. (1996). Presence of the African saber-toothed felid *Megantereon whitei* (Broom, 1937) (Mammalia, Carnivora, Machairodontinae) in Apollonia-1 (Mygdonia Basin, Macedonia, Greece). *Journal of Archaeological Science 23*, 869–872.

Matschie, P. (1900). Geographische Formen der Hyänen. (*Hyaena syrica* Mtsch. Terra typica: Antakya/Antiochia). *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1900*, 18–58.

Matthews, L.H. (1939). Reproduction in the spotted hyaena, *Crocuta crocuta* (Erxleben). *Philosophical Transactions of the Royal Society of London B 230,* 1–78.

Mazza, P.P.A., & Ventra, D. (2011). Pleistocene debris-flow deposition of the hippopotamus-bearing collecurti bonebed (Macerata, Central Italy): Taphonomic and paleoenvironmental analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology 310*, 296–314.

Mein, P. (1958). Les mammifères de la faune sidérolithique de Vieux-Collonges. *Nouvelles Archives du Muséum d 'Histoire Naturelle, Lyon 5*, 1–122.

Mein, P. (1979). Rapport d'activité du groupe de travail vertébrés mise à jour de la biostratigraphie du Néogène basee sur les mammifères*. Annales Géologiques des Pays Helléniques 1979*, 1367–1372.

Mein, P. (1989). Updating of MN zones. In: Lindsay, E.H., Fahlbusch, V., & Mein, P. (eds). European neogene mammal chronology. Plenum Press, New York, pp 73–90.

Melazde, G.K. (1967). *Hipparion* fauna of Arkneti and Bazaleti. 201 pp. Metsniereba, Tbilisi. (In Russian)

Meyer, F.A. (1793). Systematisch summarische Uebersicht der neuesten zoologischen Entdeckungen. 187 pp. Dykischen, Leipzig.

Mills, M.G.L. (1977). Foraging behaviour of the brown hyaena (*Hyaena brunnea* Thunberg, 1820) in the southern Kalahari*. Zeitschrift für Tierpsychologie 48*, 113–141

Mills, M.G.L. (1978). The comparative socio-ecology of the Hyaenidae. *Carnivore 1*, 1–7.

Mills, M.G.L. (1982a). Factors affecting group size and territory size of the brown hyaena, *Hyaena brunnea* in the southern Kalahari. *Journal of Zoolology, London 198*, 39–51.

Mills, M.G.L. (1982b*). Hyaena brunnea*. *Mammal Species 194*, 1–5.

Mills, M.G.L. (1982c). The mating system of the brown hyaena, *Hyaena brunnea* in the southern Kalahari. *Behavioral Ecology and Sociobiology 10,* 131–136.

Mills, M.G.L. (1982d). Notes on age determination, growth and measurements of brown hyaenas *Hyaena brunnea* from the Kalahari Gemsbok National Park. *Koedoe 25*, 55–61.

Mills, M.G.L. (1983). Behavioural mechanisms in territory and group maintenance of the brown hyaena, *Hyaena brunnea*, in the southern Kalahari. *Animal Behaviour 31*, 503–510.

Mills, M.G.L. (1989). The comparative behavioral ecology of hyenas: the importance of diet and food dispersion. In: Gittleman, J.L. (ed). Carnivore behavior, ecology and evolution. Chapman and Hall, London, pp 125–142.

Mills, M.G.L. (1990). Kalahari hyaenas: the comparative behavioural ecology of two species. 304 pp. Unwin Hyman, London.

Mills, M.G.L., & Biggs, H.C. (1993). Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. *Symposia of the Zoological Society of London 65*, 253–268.

Mills, M.G.L., & Gorman, M.L. (1987). The scent -marking behaviour of the spotted hyaena *Crocuta crocuta* in the southern Kalahari. *Journal of Zoolology, London 212*, 483–497.

Mills, M.G.L., & Hofer, H. (1998). Hyaenas: status survey and conservation action plan (Vol. 41). 154 pp. Osprey Publishing, Gland.

Mills, M.G.L., & Maude, G. (2005). The comparative feeding ecology of the brown hyaena in a cattle area and a national park in Botswana. *South African Journal of Wildlife Research 35*, 201–214.

Mills, M.G.L., & Mills, M.E. (1978). The diet of the brown hyaena *Hyaena brunnea* in the southern Kalahari. *Koedoe 21*, 125–149.

Mills, M.G.L., & Mills, M.E.J. (1977). An analysis of bones collected at hyaena breeding dens in the Kalahari Gemsbok National Park. *Annals of the Transvaal Museum 30*, 145–159.

Mills, M.G.L., & Mills, M.E.J. (1982). Factors affecting the movement patterns of brown hyaenas, *Hyaena brunnea*, in the southern Kalahari. *South African Journal of Wildlife Research 12*, 111–117.

Mills, M.G.L., Gorman, M.L.K. & Mill, M.E.J. (1980). The scent marking behaviour of the brown hyaena, *Hyaena brunnea*, in the southern Kalahari. *South African Journal of Zoology 15*, 240–248.

Morales, J. (2016). Los carnívoros de Villarroya. In: Alberdi, M.T., Azanza, B., & Cervantes, E., (eds). Villarroya, yacimiento clave de la paleontología riojana. Insituto de Estudios Riojanos, Logroño, pp 119–142.

Morales, J., Nieto, M., Köhler, M., & Moyà-Solà, S. (1999). Large mammals from the Vallesian of Spain. In: Agustí, J., Rook, L., & Andrews, P. (eds). Hominoid evolution and climatic change in Europe. The evolution of Neogene terrestrial ecosystems in Europe, volume 1. Cambridge University Press, Cambridge, pp 113–126.

Moullé, P.E. (1992). Les grands mammifères du Pléistocène inférieur de la grotte du vallonnet (roquebrune-cap-martin, alpes maritimes). Étude paléontologique des Carnivores, Équidés, Suidés et Bovidés. Ph.D. Dissertation, Muséum National d'Histoire Naturelle, Paris.

Moyà-Solà, S. (1983). Los Boselaphini (Bovidae Mammalia) del Neógeno de la Península Ibérica. Ph.D. Dissertation, Universitat Autònoma de Barcelona.

Muñoz, A., Pueyo, E.L., Laplana, C., & Parés, J.M. (2016). Geologia y estratigrafía. In: Alberdi, M.T., Azanza, B., & Cervantes, E. (eds). Villarroya, yacimiento clave de la Paleontología Riojana. Insituto de Estudios Riojanos, Logroño, pp 67–84.

Munthe, K. (1989). The skeleton of the Borophaginae (Carnivora, Canidae): morphology and function. *University of California Publications in Geological Sciences 133,* 1–115.

Murie, J. (1871). On the Female Generative Organs, Viscera, and Fleshy Parts of *Hyæna brunnea*, Thunberg. *The Transactions of the Zoological Society of London 7*, 503–512.

Nealen, P.M., & Ricklefs, R.E. (2001). Early diversification of the avian brain: Body relationship. *Journal of Zoology 253*, 391–404.

Nel, J.A.J., & Bothma, J.D.P. (1983). Scent marking and midden use by aardwolves (*Proteles cristatus*) in the Namib Desert. *African Journal of Ecology 21*, 25–39.

Olive, F. (2006). Evolution of Plio Pleistocene larger Carnivores in Africa and Western Europe. *L'Anthropologie 110*, 850–869.

Owens, D.D., & Owens, M.J. (1979a). Notes on social organization and behavior in brown hyenas (*Hyaena brunnea*). *Journal of Mammalogy 60,* 405–408.

Owens, D.D., & Owens, M.J. (1979b). Communal denning and clan associations in brown hyenas, *Hyaena brunnea* Thunberg, of the central Kalahari Desert, Botswana. *African Journal of Ecology 17*, 35–44.

Owens, D.D., & Owens, M.J. (1984). Helping behaviour in brown hyaenas. *Nature 308*, 843–845.

Owens, M.J., & Owens, D.D. (1978). Feeding ecology and its influence on social organization in Brown hyenas (*Hyaena brunnea*, Thunberg) of the Central Kalahari Desert. *East African Wildlife Journal 16*, 113–135.

Ozansoy, F. (1965). Étude des gisements continentaux et des mammifères du Cénozoïque de Turquie. *Mémoires de la Société Géologique de France 102*, 1–92.

Palgrave, K.C. (2002). Trees of southern Africa. New edition revised and updated by Meg Coates Palgrave. 118 pp. Struik*,* Cape Town.

Palmqvist, P., Martínez-Navarro, B., Pérez-Claros, J.A., Torregrosa, V., Figueirido, B., Jiménez-Arenas, J.M., Espigares, M.P., Ros-Montoya, S., & De Renzi, M. (2011). The giant hyena *Pachycrocuta brevirostris*: Modelling the bone-cracking behavior of an extinct carnivore. *Quaternary International 243*, 61–79.

Palombo, M.R. (2014). Desconstructing mammal dispersals and faunal dynamics in SW Europe during the Quaternary. *Quaternary Science Reviews 96*, 50–71.

Paulli, S. (1900). Über die Pneumaticität des Schädels bei den Säugetieren. Eine morphologische Studie III. Über die Morphologie des Siebbeins und Pneumaticität bei den Insectivoren, Hyracoideen, Chiropteren, Carnivoren, Pinnipedien, Edentates, Rodentiern, Prosimien und Primaten. *Gegenbaurs Morphologisches Jahrbuch 28*, 483–564.

Pavlow, M. (1908). Quelques carnivores fossils du gouvernement de Kherson et de Bessarabie. *Mémoires de la Sociéte des Naturalistes de la Nouelle-Russie, Odessa 32*, 27–48.

Pérez de Perceva, M.A., Manteca Martínez, J.I., & López-Morell, M.A. (2015). Historia de la minería de Cueva Victoria. *Mastia 11–13,* 47–58.

Pérez-Cuadrado, J.L., & Ferrández, C. (1992). Cueva Victoria: cubil de carroñeros. In: Gibert, J., & Gibert, G.C. (eds). Presencia humana en el Pleistoceno inferior de Granada y Murcia. Museo de Prehistoria y Paleontología" J. Gibert", Orce, pp 133–142.

Petter, G., & Howell, F.C. (1989). Une nouvelle espèce du genre *Crocuta* Kaup (Mammalia, Carnivora, Hyaenidae) dans la faune pliocène de Laetoli (Tanzanie): *Crocuta dietrichi* n. sp.; origine du genre. *Comptes Rendus de l'Académie des Sciences, Paris 308*, 1031–1038.

Pienaar, U.D.V. (1969). Predator-prey relationships amongst the larger mammals of the Kruger National Park. *Koedoe 12*, 108–184

Pilgrim, G.E. (1910). Notices of new mammalian genera and species from the Tertiaries of India. *Records of the Geological Survey of India 40*, 63–71.

Pilgrim, G.E. (1931). Catalogue of the Pontian Carnivora of Europe in the Department of Geology. 174 pp. British Museum of Natural History, London.

Pilgrim, G.E. (1932). The fossil Carnivora of India. *Paleontologica Indica 18*, 1–232.

Pocock, R.I. (1916). On some of the external structural characters of the striped hyaena (*Hyaena hyaena*) and related genera and species. *Journal of Natural History 17*, 330–343.

Pocock, R.I. (1929). Carnivora, 14th ed. Encyclopaedia Brittanica 14, pp 896-900.

Pocock, R.I. (1934). The races of the striped and brown hyaenas. *Journal of Zoology 104*, 799–825.

Pocock, R.I. (1941). The Fauna of British India. Mammalia Vol II. 503 pp. Taylor and Francis, London.

Pons-Moyà, J. (1981). El *Canis etruscus* Major (Carnivora, Mammalia) del Villafranquiense terminal de la Cueva Victoria (Murcia, España). *Endins 8*, 43–46.

Pons-Moyà, J. (1982). Hyaenidae (Carnivora, Mammalia) del Pleistoceno inferior de la Cueva Victoria (Murcia, España). *Endins 9*, 45–48.

Pons-Moyà, J. (1983). Presencia de *Lynx spelaea* (Fissipeda, Mammalia) en el Pleistoceno inferior de la Península Ibérica. *Paleontologia i Evolució 18,* 39–42.

Pons-Moyà, J., & Moyà-Solà, S. (1978). La fauna de Carnívoros del Pleistoceno medio (Mindel) de la Cueva Victoria (Cartagena, España). *Acta Geológica Hispanica 13*, 54–58.

Postigo Mijarra, J.M., Burjachs, F., Gómez Manzaneque, F., & Morla, C. (2007). A palaeoecological interpretation of the lower–middle Pleistocene Cal Guardiola site (Terrassa, Barcelona, NE Spain) from the comparative study of wood and pollen samples. *Review of Paleobotany and Palynology 146*, 247–264.

Pournelle, G.H. (1965). Observations on birth and early development of the spotted hyaena. *Journal of Mammalogy 46*, 503.

Pueyo, E.L., Muño, A., Laplana, C., & Parés, J.M. (2016). Datación magnetoestratigráfica de la Cuenca de Villarroya. In: Alberdi, M.T., Azanza, B., & Cervantes, E. (eds). Villarroya, yacimiento clave de la Paleontología Riojana. Insituto de Estudios Riojanos, Logroño, pp 229–246.

Qiu Z.X. (1987). Die Hyaeniden aus dem Ruscinium und Villafranchium Chinas. *Münchner Geowissenschaftliche Abhandlungen A 9*, 1–108.

Qiu Z.X. (1989). The Chinese Neogene Mammalian biochronology: Its correlation with the European Neogene mammalian zonation. In: Lindsay, E.H., Fahlbusch, V., & Mein, P. (eds). European Neogene Mammal Chronology. Plenum Press, New York, pp 527–556.

Qiu Z.X., Deng, T., & Wang, B.Y. (2004). Early Pleistocene mammalian fauna from Longdan, Dongxiang, Gansu, China. *Palaeontologia Sinica C 27*, 1–198.

Qiu Z.X., Huang, W., & Zuo, Z. (1979). Hyaenidae of Qingyang (K'ingyang) Hipparion fauna. *Vertebrata PalAsiatica 17*, 200–211.

Qiu Z.X., Ye J. & Cao J. (1988a) A new species of *Percrocuta* from Tongxin, Ningxia. *Vertebrata PalAsiatica 26*, 116–127.

Qiu, Z.X., Xie, J., & Yan, D. (1988b). Discovery of the skull of *Dinocrocuta gigantea*. *Vertebrata PalAsiatica 26*, 128–138.

Racey, P.A., & Skinner, J.D. (1979). Endocrine aspects of sexual mimicry in spotted hyaenas *Crocuta crocuta*. *Journal of Zoology 187*, 315–326.

Radinsky, L.B. (1969). Outlines of canid and felid brain Evolution. *Annals of the New York Academy of Sciences 167*, 277–288.

Radinsky, L.B. (1971). An example of parallelism in carnivore brain evolution. *Evolution 25*, 518–522.

Radinsky, L.B. (1975). Evolution of the felid brain. *Brain, Behavior and Evolution 11*, 214–254.

Radinsky, L.B. (1977). Brains of early carnivores. *Paleobiology 3*, 333–349.

Rensberger, J.M. (1999). Enamel microstructural specialization in the canine of the spotted hyena, *Crocuta crocuta*. *Scanning Microscopy 13*, 343–361.

Rensberger, J.M., & Stefen, C. (2006). Functional differentiations of the microstructure in the upper carnassial enamel of the spotted hyena. *Palaeontographica Abteilung A 278*, 149–162.

Rensberger, J.M., & Wang, X. (2005). Microstructural reinforcement in the canine enamel of the hyaenid *Crocuta crocuta*, the felid *Puma concolor* and the late Miocene canid *Borophagus secundus*. *Journal of Mammalian Evolution 12*, 379–403.

Richardson, P.R.K. & Bearder, S.K. (1984). The aardwolf. In: Macdonald, D.W. (ed). The encyclopaedia of mammals, Vol 1. George Allen and Unwin, London, pp 158–159.

Richardson, P.R.K. & Levitan, C.D. (1994). Tolerance of aardwolves to defence secretions of *Trinervitermes trinervoides*. *Journal of Mammalogy 75*, 84–91.

Richardson, P.R.K. (1987a). Aardwolf: the most specialized myrmecophagous mammal? South *African Journal of Science 83*, 643–646.

Richardson, P.R.K. (1987b). Food consumption and seasonal variation in the diet of the aardwolf *Proteles cristatus* in southern Africa. *Zeitschrift für Säugetierkunde 52*, 307–325.

Richardson, P.R.K. (1987c). Aardwolf mating system: overt cuckoldry in an apparently monogamous mammal. *South African Journal of Science 83*, 405–410.

Richardson, P.R.K. (1990). Scent marking and territoriality in the aardwolf. In: Macdonald, D.W., Muller-Schwarze, D., & Natynczuk, S.E. (eds). Chemical signals in vertebrates. Oxford University Press, Oxford, pp 378–387.

Richardson, P.R.K. (1991). Territorial significance of scent-marking during the non -mating season in the aardwolf *Proteles cristatus* (Carnivora: Protelidae). *Ethology 87,* 9–27.

Rieger, I. (1979). A review of the biology of striped hyaenas, *Hyaena hyaena* (Linné, 1758). *Säugetierkundliche Mitteilungen 27*, 81–95.

Rieger, I. (1981). *Hyaena hyaena*. *Mammalian Species 150*, 1–5.

Roberts, T.J. (1977). The mammals of Pakistan. 525 pp. E. Benn, London.

Roca, E., & Guimerà, J. (1992). The Neogene structure of the eastern Iberian margin: structural constraints on the crustal evolution of the Valencia trough (western Mediterranean). *Tectonophysics 203*, 203–218.

Roca, E., & Muñoz, J.A. (2010). De Montserrat a la Conca de Barcelona: l'obertura de la Mediterrània. In: Roca i Adrover, A., & Miranda i Canals, J. (eds). Atles geològic de Catalunya. Generalitat de Catalunya, Barcelona, pp 146–149.

Roca, E., Sans, M., Cabrera, L., & Marzo, M. (1999). Oligocene to Middle Miocene evolution of the central Catalan margin (northwestern Mediterranean). *Tectonophysics 315*, 209–229.

Rögl, F., & Steininger F.F. (1983). Vom Zerfall der Tethys zu Mediterran und Paratethys-Die neogene Paläographie und Palinspastik des zirkum-mediterranen Raumes. *Annalen des Naturhistorisches Museums Wien 85A*, 135–163.

Rohland, N., Pollack, J.L., Nagel, D., Beauval, C., Airvaux, J., Pääbo, S., & Hofreiter, M. (2005). The population history of extant and extinct hyenas. *Molecular Biology and Evolution 22*, 2435–2443.

Rook, L., Ferretti, M.P., Arca, M., & Tuveri, C. (2004). *Chasmaporthetes melei* n. sp., an endemic hyaenid (Carnivora, Mammalia) from the Monte Tuttavista fissure fillings (Late Pliocene to Early Pleistocene; Sardinia, Italy). *Rivista Italiana di Paleontologia e Stratigrafia 110*, 707–714.

Rosevear, D.R. (1974). Carnivores of west Africa. 548 pp. British Museum of Natural History, London.

Roth, J., & Wagner, J.A. (1854). Die fossilen Knochenüberreste von Pikermi in Griechenland. *Abhandlungen der Bayerischen Akademie der Wissenschaften 7*, 371–464.

Rothschild, W. (1902). Two new subspecies of *Proteles*. *Novitates Zoologicae 9*, 443.

Sakai, S.T., Arsznov, B.M., Lundrigan, B.L., & Holekamp, K.E. (2011). Brain Size and Social Complexity: A Computed Tomography Study in Hyaenidae. *Brain, Behavior and Evolution 77*, 91–104.

Santafé-Llopis, J.V., & Casanovas-Cladellas, M.L. (1982). Los rinocerótidos (Mammalia, Perissodactyla) del Turoliense del Penedès (Piera, Barcelona). *Butlletí Informatiu de l'Institut de Paleontologia de Sabadell 14*, 39–47.

Sardella, R., & Petrucci, M. (2012). The earliest Middle Pleistocene *Crocuta crocuta* (Erxleben, 1777) at Casal Selce (Rome, Italy). *Quaternary Internacional 267*, 103–110.

Sauqué, V., Rabal-Garcés, R., Madurell-Malaperia, J., Gisbert, M., Zamora, S., de Torres, T., & Cuenca-Bescós, G. (2017). Pleistocene cave hyenas in the Iberian Peninsula: new insights from Los Aprendices cave (Moncayo, Zaragoza). *Palaeontologia Electronica 20*, 1–38.

Savage, D.E. & Russell, D. (1983). Mammalian paleofaunas of the world. 432 pp. Addison-Wesley, New York.

Schlosser, M. (1890). Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des europäischen Tertiärs. III. *Beiträge zur Paläontologie un GeologieÖsterreich-Ungarns und des Orients 8*, 1–107.

Schmidt-Kittler, N. (1976). Raubtiere aus dem Jungtertiär Kleinasiens. *Palaeontographica Abteilung A 155*, 1–131.

Schultz, W.C. (1966). Breeding and hand-rearing of brown hyaenas at Okahandja Zoopark. *International Zoo Year Book 6*, 173–176.

Sears, K.E., Finarelli, J.A., Flynn, J.J., & Wyss, A.R. (2008). Estimating body mass in New World ‘‘monkeys’’ (Platyrrhini, Primates) from craniodental measurements, with a consideration of the Miocene platyrrhine, *Chilecebus carrascoensis*. *American Museum Novitates 3617*, 1–29.

Semenov, Y. (1988). *Ictitherium spelaeum* sp.n. (Carnivora, Viverridae) from Middle Sarmat of the Ukraine. *Vestnik Zoologii 1988*, 45–49.

Semenov, Y. (1989). Ictitheres and morphologically related hyaenas from the Neogene of the USSR. 178 pp. Naukova Dumka, Kiev.

Semenov, Y. (2008). Taxonomical reappraisal of “ictitheres” (Mammalia, Carnivora) from the Late Miocene of Kenya. *Comptes Rendus Palevol 7*, 529–539.

Sheng, G.L., Soubrier, J., Liu, J.Y., Werdelin, L., Llamas, B., Thomson, V.A., Tuke, J., Wu, L.J., Hou, X.D., Chen, Q.J., Lai, X.L., & Cooper, A. (2014). Pleistocene Chinese cave hyenas and the recent Eurasian history of the spotted hyena, *Crocuta crocuta*. *Molecular Ecology 23*, 522–533.

Siegfried, W.R. (1984). An analysis of fecal pellets of the brown hyena, *Hyaena brunnea*, on the Namib coast, South Africa. *South African Journal of Zoology 19*, 61–61.

Sillero-Zubiri, C., & Gottelli, D. (1992). Population ecology of spotted hyaena in an equatorial mountain forest. *African Journal of Ecology 30*, 292–300.

Sinusía C., Pueyo E.L., Azanza B. & Pocoví A. (2004). Datación magnetoestratigráfica del yacimiento paleontológico de Puebla de Valverde (Teruel). *GeoTemas 6*, 339–342.

Skinner, J.D. (1976). Ecology of the brown hyaena *Hyaena brunnea* in the Transvaal with a distribution map for southern Africa. *South African Journal of Science 72*, 262–269.

Skinner, J.D. (2006). Bone collecting by hyaenas: a review. *Transactions of the Royal Society of South Africa 61*, 4–7.

Skinner, J.D., & Chimimba, C.T. (2005). The mammals of the southern African sub-region. 814 pp. Cambridge University Press, Cambridge.

Skinner, J.D., & Ilani, G. (1979). The striped hyaena *Hyaena hyaena* of the Judean and Negev Deserts and a comparison with the brown hyaena *H. brunnea*. *Israel Journal of Zoolology 28*, 229–232.

Skinner, J.D., & Van Aarde, R.J. (1981). The distribution and ecology of the brown hyaena *Hyaena brunnea* and spotted hyaena *Crocuta crocuta* in the central Namib Desert. *Madoqua 12*, 231–239.

Skinner, J.D., Funston, P.J., Van Aarde, R.J., Van Dyk, G., & Haupt, M.A. (1992). Diet of spotted hyaenas in some mesic and arid southern African game reserves adjoining farmland. *South African Journal of Wildlife Research 22*, 119–121.

Skinner, J.D., Henschel, J.R., & Van Jaarsveld, A.S. (1986). Bone-collecting habits of spotted hyaenas *Crocuta crocuta* in the Kruger National Park. *South African Journal of Zoology 21*, 303–308.

Sliwa, A. (1996). A functional analysis of scent marking and mating behaviour in the aardwolf (*Proteles cristatus*, Sparrman 1783). Ph.D. Dissertation, University of Pretoria.

Sliwa, A., & Richardson, P.R. (1998). Responses of aardwolves, *Proteles cristatus*, Sparrman 1783, to translocated scent marks. *Animal Behaviour 56,* 137–146.

Smale, L., Nunes, S. & Holekamp, K.E. (1997). Sexually dimorphic dispersal in mammals: Patterns, causes, and consequences. In: Slater, P.J.B., Rosenblatt, M., Milinski, M. & Snowdon, C.T. (eds). Advances in the study of behavior, Vol 26. Academic Press, New York, pp 181–250.

Smith, J.E., Kolowski, J.M., Graham, K.E., Dawes, S.E., & Holekamp, K.E. (2008). Social and ecological determinants of fission–fusion dynamics in the spotted hyaena. *Animal Behaviour 76*, 619–636.

Smith, J.E., Memenis, S.K., & Holekamp, K.E. (2007). Rank-related partner choice in the fission-fusion society of spotted hyenas (*Crocuta crocuta*). *Behavioral Ecology and Sociobiology 61*, 753–765.

Smithers, R.H., & Wilson, V.J. (1979). A check list and atlas of the mammals of Zimbabwe Rhodesia. 193 pp. Trustees of the National Museum of Rhodesia, Salisbury.

Smithers, R.H.N. (1971). The mammals of Botswana. *Memoirs of the National Museum, Rhodesia 4*, 1–340.

Smithers, R.H.N. (1983). The mammals of the Southern African subregion. 736 pp. University of Pretoria, Pretoria.

Smuts, G.L. (1979). Diet of lions and spotted hyaenas assessed from stomach contents. *South African Journal of Wildlife Research 9*, 19–25.

Solounias, N. (1981). The Turolian fauna from the island of Samos, Greece. *Contributions to Vertebrate Evolution 6*, 1–232.

Soria, D. (1980). "*Percrocuta* y *Adcrocuta*"(Hyaenidae, Mammalia) en el Mioceno superior del área de Teruel. *Estudios Geológicos 36*, 143–162.

Sparrman, A. (1783). Resa till Goda Hopps-Udden Södra Polkretsen och Omkring Jordklotet sant till Hottentott- och Caffer-landen åren 1772-76. 766 pp. A.J. Nordström, Stockholm.

Stefen, C. (1997). Differentiations in Hunter-Schreger bands of carnivores. In: Koenigswald, W.V. & Sander, P.M. (eds). Tooth enamel microstructure. Balkema, Rotterdam, pp 123–136.

Stefen, C. (1999). Enamel microstructure of recent and fossil Canidae (Carnivora: Mammalia). *Journal of Vertebrate Paleontology 19,* 576–587.

Stefen, C. (2001). Enamel structure of arctoid carnivora: Amphicyonidae, Ursidae, Procyonidae, and Mustelidae. *Journal of Mammalogy 82*, 450–462.

Stefen, C., & Rensberger, J. M. (1999). The specialized structure of hyaenid enamel: description and development within the lineage—including percrocutids. *Scanning Microscopy 13,* 363–380.

Stoeckelhuber, M., Sliwa, A., & Welsch, U. (2000). Histo-physiology of the scent-marking glands of the penile pad, anal pouch, and the forefoot in the aardwolf (*Proteles cristatus*). *The Anatomical Record 259,* 312–326.

Stromer, E. (1931). Reste süsswasser- und landbewohnender Wirberltiere aus den Diamantefeldern Klein-Namaqualandes (Südwest-Afrika). *Sitzungsberichte der bayerischen Akademie der Wissenschaften zu München 1931*, 17–47.

Stuart, C.T., & Shaughnessy, P.D. (1984). Content of *Hyaena brunnea* and *Canis mesomelas* scats from southern coastal Namibia. *Mammalia 48*, 611–612.

Sutcliffe, A.T. (1970). Spotted hyaena: crusher, gnawer, digester and collector of bones. *Nature 227*, 1110–1113.

Swanson, E.M., Holekamp, K.E., Lundrigan, B.L., Arsznov, B.M., & Sakai, S.T. (2012). Multiple determinants of whole and regional brain volume among terrestrial carnivorans. *PLOS ONE 7*, e38447.

Szykman, M., Engh, A.L., Van Horn, R.C., Funk, S., Scribner, K.T., & Holekamp, K.E. (2001). Association patterns between male and female spotted hyenas reflect male mate choice. *Behavioral Ecology and Sociobiology 50*, 231–238.

Tanner, J.M., Dumont, E.R., Sakai, S.T., Lundrigan, B.L., & Holekamp, K.E. (2008). Of arcs and vaults: the biomechanincs of bone-cracking in spotted hyenas (*Crocuta crocuta*). *Biological Journal of the Linnean Society 95*, 246–255.

Theis, K.R., Greene, K.M., Benson-Amram, S.R., & Holekamp, K.E. (2007). Sources of variation in the long-distance vocalizations of spotted hyenas. *Behaviour 144*, 557–584.

Thenius, E. (1966). Zur Stammesgeschichte der Hyänen (Carnivora, Mammalia). *Zeitschrift für Säugetierkunde 31*, 293–300.

Thomas, H., Bernor, R.L., & Jaeger, J.J. (1982). Origines du peuplement mammalien en Afrique du Nord. *Géobios 15*, 283–97.

Thunberg, C.P. (1820). Beskrifning och teckning på ett nytt species, *Hyaena brunnea. Kongliga Vetenskapsakademiens Handlingar för år 1820,* 59–65.

Tilson, R.L. & Henschel, J.R. (1986). Spatial arrangement of spotted hyaena groups in a desert environment, Namibia. *African Journal of Ecology 24*, 173–180.

Tilson, R.L., Von Blottnitz, F., & Henschel, J.R. (1980). Prey selection by spotted hyaenas (*Crocuta crocuta*) in the Namib Desert. *Madoqua 12*, 41–49.

Toerien, M.J. (1952). The fossil hyenas of the Makapansgat valley. *South African Journal of Science 48*, 293–300.

Tomes, C.S. (1906). On the minute structure of the teeth of credonts, with special reference to their suggested resemblance to marsupials. *Proceedings of the Zoological Society of London 1906*, 45–58.

Torre, D. (1989). *Plioviverrops faventinus* n. sp., a new carnivore of Late Messinian age. *Bollettino della Società Paleontologica Italiana 28*, 323–327.

Trouessart, E.L. (1897). Catalogus Mammalium tam Vivientum quam Fossilium. 664 pp. R. Friedländer, Berlin.

Tseng, Z.J. (2009). Cranial function in the late Miocene *Dinocrocuta gigantea* (Mammalia, Carnivora) revealed by comparative finite element analysis. *Biological Journal of the Linnean Society 96*, 51–67.

Tseng, Z.J. (2011). Variation and implications of intra-dentition Hunter-Schreger band pattern in fossil hyaenids and canids (Carnivora, Mammalia). *Journal of Vertebrate Paleontology 31*, 1163–1167.

Tseng, Z.J. (2012). Connecting Hunter-Schreger Band microstructure to enamel microwear features: New insights from durophagous carnivores. *Acta Palaeontologica Polonica 57*, 473–484.

Tseng, Z.J., & Wang, X. (2007). The first record of the Late Miocene *Hyaenictitherium hyaenoides* Zdansky (Carnivora: Hyaenidae) in Inner Mongolia and an evaluation of the genus. *Journal of Vertebrate Paleontology 27*, 699–708.

Tseng, Z.J., & Wang, X. (2010). Cranial functional morphology of fossil dogs and adaptation for durophagy in *Borophagus* and *Epicyon* (Carnivora, Mammalia). *Journal of Morphology 271*, 1386–1398.

Tseng, Z.J., & Wang, X. (2011). Do convergent ecomorphs evolve through convergent morphological pathways? Cranial shape evolution in fossil hyaenids and borophagine canids (Carnivora, Mammalia). *Paleobiology 37*, 470–489.

Tseng, Z.J., Antón, M., & Salesa, M.J. (2011). The evolution of the bone-cracking model in carnivorans: cranial functional morphology of the Plio-Pleistocene cursorial hyaenid *Chasmaporthetes lunensis* (Mammalia: Carnivora). *Paleobiology 37*, 140–156.

Tseng, Z.J., Li, Q., & Wang, X. (2013). A new cursorial hyena from tibet, and analysis of biostratigraphy, paleozoogeography, and dental morphology of *Chasmaporthetes* (Mammalia, Carnivora). *Journal of Vertebrate Paleontology 33*, 1457–1471.

Tseng, Z.J., Wang, X., Li, Q., & Xie, G. (2015). Pliocene bone-cracking Hyaeninae (Carnivora, Mammalia) from the Zanda Basin, Tibet Autonomous Region, China. *Historical Biology 28*, 69–77.

Turner, A. (1984). The interpretation of variation in fossil specimens of spotted hyaena (*Crocuta crocuta* Erxleben, 1777) from Sterkfontein Valley sites (Mammalia: Carnivora). *Annals of the Transvaal Museum 33*, 399–418.

Turner, A. (1990). The evolution of the guild of larger terrestrial carnivores in the Plio-Pleistocene of Africa. *Geobios 23*, 349–368.

Turner, A. (1995). The Villafranchian large carnivore guild: geographic distribution and structural evolution. *Il Quaternario 8*, 349–356.

Turner, A. (2001). Remains of *Pachycrocuta brevirostris* (Carnivora, Hyaenidae) from the lower Pleistocene site of Untermassfeld. In: Kahlke, R.D. (ed). Das Pleistozän von Untermassfeld bei Meiningen (Thüringen), volume 2. Römisch-Germaisches Zentralmuseum, Bonn, pp 673–690.

Turner, A., & Antón, M. (1996). The giant hyaena, *Pachycrocuta brevirostris* (Mammalia, Carnivora, Hyaenidae). *Geobios 29*, 455–468.

Turner, A., & Antón, M. (2004). Evolving eden: an illustrated guide to the evolution of the African large mammal fauna. 304 pp. Columbia University Press, New York.

Turner, A., Antón, M., & Werdelin, L. (2008). Taxonomy and evolutionary patterns in the fossil Hyaenidae of Europe. *Geobios 41*, 677–687.

Valenciano, A., Baskin, J.A., Abella, J., Pérez-Ramos, A., Álvarez-Sierra, M.Á., Morales, J., & Hartstone-Rose, A. (2016). *Megalictis*, the bone-crushing giant mustelid (Carnivora, Mustelidae, Oligobuninae) from the Early Miocene of North America. *PLoS One 11*, e0152430.

Valenzuela, A. (1970). Un karst fósil y depósitos de minerales de origne kárstico al Sureste de la zona bétoca. In: Comunicaciones I Congreso Nacional de Espeleología. Ayuntamiento de Barcelona, Barcelona, pp 61–77.

Van Dam, J.A., Abdul Aziz, H., Álvarez-Sierra, M.A., Hilgen, F.J., Van den Hoek Ostende, L.W., Lourens, L.J., Mein, P., Van der Meulen, A.J., & Pélaez-Campomanes, P. (2006). Long-period astronomical forcing of mammal turnover. *Nature 443*, 687–691.

Van Dam, J.A., Alcalá, L., Alonso-Zarza, A., Calvo, J.P., Garcés, M., & Krijgsman, W. (2001). The upper Miocene mammal record from the Teruel-Alfambra region (Spain). The MN system and continental stage/age concepts discussed. *Journal of Vertebrate Paleontology 21*, 367–385.

Van der Made, J., Montoya, P., & Alcalá, L. (1992). *Microstonyx* (Suidae, Mammalia) from the Upper Miocene of Spain. *Geobios 25*, 395–413.

Van Jaarsveld, A.S., & Skinner, J.D. (1987). Spotted hyaena monomorphism: an adaptive "phallusy". *South African Journal of Sciences 83*, 612–615.

Van Jaarsveld, A.S., Skinner, J.D., & Lindeque, M. (1988). Growth, development and parental investment in the spotted hyaena, *Crocuta crocuta*. *Journal of Zoology 216*, 45–53.

Van Valkenburgh, B. (1989). Carnivore dental adaptations and diet: a study of trophic diversity within guilds. In: Gitleman, J.L. (ed). Carnivore Behavior, Ecology and Evolution. Cornell University Press, Ithaca, New York, pp 410–436.

Van Valkenburgh, B. (1996). Feeding behavior in free-ranging African carnivores. *Journal of Mammalogy 77*, 240–254.

Van Valkenburgh, B. (1999). Major patterns in the history of carnivorous mammals. *Annual Review of Earth and Planetary Sciences 27*, 463–493.

Van Valkenburgh, B. (2007). Déjà vu: the evolution of feeding morphologies in the Carnivora. *Integrative and Comparative Biology 47*, 147–163.

Van Valkenburgh, B., Sacco, T., & Wang, X. (2003). Chapter 7: pack hunting in Miocene borophagine dogs: evidence from craniodental morphology and body size. *Bulletin of the American Museum of Natural History 279*, 147–162.

Veron, G. (1995). La position systématique de *Cryptoprocta ferox* (Carnivora). Analyse cladistique des caractères morphologiques de carnivores Aeluroidea actuels et fossiles. *Mammalia 59*, 551–582.

Villalta Comella, J.F., & Crusafont Pairó, M. (1943). Nuevas aportaciones al conocimiento de los carnívoros pontienses del Vallés-Panadés. *Boletín del Instituto Geológico y Minero de España 65*, 1–192.

Villalta Comella, J.F., & Crusafont Pairó, M. (1945). Nuevas aportaciones al conocimiento de los carnívoros Pontienses del Vallés-Penedés. *Publicaciones del Instituto Geológico 7*, 81–121.

Villalta Comella, J.F., & Crusafont Pairó, M. (1946). Les gisements de Mammifères du Néogène espagnol. III. Bassin du Vallés-Penadés (Catalogne). Pontien*. Comptes Rendus Sommaires de la Societé Géologique de France 1946*, 224–227.

Villalta Comella, J.F., & Crusafont Pairó, M. (1948). Nuevas aportaciones al conocimiento de los carnívoros pontienses del Vallés-Penedés. *Miscelanea Almera 7*, 81–121.

Villalta, J.F. (1952). Contribución al conocimiento de la fauna de Mamíferos Fósiles del Plioceno de Villarroya (Logroño). *Boletín del Instituto Geológico y Minero de España 64*, 3–204.

Viranta, S., & Werdelin, L. (2003). Carnivora. In: Fortelius, M., Kappelman, J., Sen, S., & Bernor, R.L. (eds). Geology and Paleontology of the Miocene Sinap Formation, Turkey. Columbia University Press, New York, pp 178–193.

Von Nordmann, A. (1858). Paleontologie Suedrusslands I-IV. 360 pp. H.C. Friis, Helsinki.

Wagner, A.P. (2006). Behavioral ecology of the striped hyena (*Hyaena hyaena*). Ph.D. Dissertation, Montana State University.

Wagner, A.P., Frank, L.G., & Creel, S. (2008). Spatial grouping in behaviourally solitary striped hyaenas, *Hyaena hyaena*. *Animal Behaviour 75*, 1131–1142.

Wagner, J.A. (1848). Urweltliche Säugethiere-Überreste aus Griechenland. Abhhandlungen der *Bayerischen Akademie der Wissenschaften 5*, 335–378

Wagner, P.J. (1998). A likelihood approach for evaluating estimates of phylogenetic relationships among fossil taxa. *Paleobiology 24*, 430–449.

Wahaj, S.A, Van Horn, R.C., Van Horn, T., Dreyer, R., Hilgris, R., Schwarz, J., & Holekamp, K.E. (2004). Kin discrimination in the spotted hyena (*Crocuta crocuta*): Nepotism among siblings. *Behavioral Ecology and Sociobiology 56*, 237–247.

Wang, X., R.H. Tedford, & B.E. Taylor. (1999). Phylogenetic systematics of the Borophaginae (Carnivora: Canidae). *Bulletin of the American Museum of Natural History 243*, 1–391.

Wayne, R.K., Benveniste, R.E., Janczewski, D.N., & O'Brien, S.J. (1989). Molecular and biochemical evolution of the Carnivora. In: Gittleman, J.L. (ed). Carnivore Behavior, Ecology and Evolution. Cornell University Press, Ithaca, New York, pp 465–494.

Werdelin, L. (1988a). Studies of fossil hyaenas: the genera *Thalassictis* Gervais ex Nordmann, *Palhyaena* Gervais, *Hyaenictitherium* Kretzoi, *Lycyaena* Hensel and *Palinhyaena* Qiu, Huang & Guo. *Zoological Journal of the Linnean Society 92*, 211–265.

Werdelin, L. (1988b). Studies of fossil hyaenids: the genera *Ictitherium* Roth & Wagner and *Sinictitherium* Kretzoi and a new species of *Ictitherium*. *Zoological Journal of the Linnean Society 93*, 93–105.

Werdelin, L. (1989). Constraint and adaptation in the bone-cracking canid *Osteoborus* (Mammalia: Canidae). *Paleobiology 15*, 387–401.

Werdelin, L. (1996). Community-wide character displacement in Miocene hyaenas. *Lethaia 29*, 97–106.

Werdelin, L. (1999). *Pachycrocuta* (hyaenids) from the Pliocene of east Africa. *Paläontologische Zeitschrift 73*, 157–165.

Werdelin, L. (2003). Mio-Pliocene Carnivora from Lothagam, Kenya. In: Leakey, M.G., & Harris, J.M. (eds). Lothagam: The Dawn of Humanity in eastern Africa. Columbia University Press, New York, pp 261–330.

Werdelin, L., & Barthelme, J. (1997). Brown hyena (*Parahyaena brunnea*) from the Pleistocene of Kenya. *Journal of Vertebrate Paleontology 17*, 758–761.

Werdelin, L., & Kurtén, B. (1999). *Allohyaena* (Mammalia: Carnivora): giant hyaenid from the Late Miocene of Hungary. *Zoological Journal of the Linnean Society 126*, 319–334.

Werdelin, L., & Lewis, M.E. (2005). Plio-Pleistocene Carnivora of Eastern Africa: species richness and turnover patterns. *Zoological Journal of the Linnean Society 144*, 121–144.

Werdelin, L., & Lewis, M.E. (2008). New species of *Crocuta* from the early Pliocene of Kenya, with an overview of early Pliocene hyenas of eastern Africa. *Journal of Vertebrate Paleontology 28*, 1162–1170.

Werdelin, L., & Peigné, S. (2010). Carnivora. In: Werdelin, L., & Sanders, W.J. (eds). Cenozoic mammals of Africa. University of California Press, Berkeley, pp 609–663.

Werdelin, L., & Solounias, N. (1990). Studies of fossil hyaenids: the genus *Adcrocuta* Kretzoi and the interrelationships of some hyaenid taxa. *Zoological Journal of the Linnean Society 98*, 363–386.

Werdelin, L., & Solounias, N. (1991). The Hyaenidae: taxonomy, systematics and evolution. *Fossils and Strata 30*, 1–104.

Werdelin, L., & Solounias, N. (1996). Evolutionary history of hyaenas in the Miocene of Europe and Western Asia. In: Bernor, R.L., Fahlbusch, V., & Rietschel, S. (eds). Later Neogene European biotic evolution and stratigraphic correlation. Columbia University Press, New York, pp 290–306.

Werdelin, L., & Turner, A. (1996a). Turnover in the guild of larger carnivores in Eurasia across the Miocene–Pliocene boundary. *Acta Zoologica Cracoviensia 39*, 585–592.

Werdelin, L., & Turner, A. (1996b). The fossil and living Hyaenidae of Africa: present status. In: Stewart, K.M., & Seymour, K.L. (eds). Palaeoecology and palaeoenvironments of Late Cenozoic mammals. University of Toronto Press, Toronto, pp 637–659.

Werdelin, L., Turner, A., & Solounias, N. (1994). Studies of fossil hyaenids: the genera *Hyaenictis* Gaudry and *Chasmaporthetes* Hay, with a reconsideration of the Hyaenidae of Langebaanweg, South Africa. *Zoological Journal of the Linnean Society 111,* 197–217.

White, T.E. (1941). Additions to the fauna of the Florida Pliocene. *Proceedings of the New England zoölogical club 18*, 67–70.

Winge, H. (1895). Jordfundne og nulevende rovdyr (Carnivora) fra Lagoa Samta, Minas Geraes, Brasilien. Med udsigt over rovdyrenes indbyrdes slaegtskab. *E Museo Lundii 2,* 1–103.

Wozencraft, W. C. (1989). The phylogeny of the recent Carnivora. In: Gittleman, J.L. (ed). Carnivore behavior, ecology, and evolution. Chapman and Hall, London, pp 495–535.

Wozencraft, W.C. (1993). Carnivora. In: Wilson, D.E., & Reeder, D.M. (eds). Mammal Species of the World: A Taxonomic and Geographic Reference. Smithsonian Institution Press, Washington DC, pp 279–348.

Wurster, D.H., & Benirschke, K. (1968). Comparative cytogenetic studies in the Order Carnivora. *Chromosoma 24*, 336–382.

Wyss, A.R., & Flynn, J.J. (1993). A phylogenetic analysis and definition of the Carnivora. In: Szalay, F.S., Novacek, M.J., & McKenna, M.C. (eds). Mammal phylogeny: placcentals. Springer-Verlag, New York, pp 32–52.

Yoder, A.D., Burns, M.M., Zehr, S., Delefosse, T., Veron, G., Goodman, S.M., & Flynn, J.J. (2003). Single origin of Malagasy Carnivora from an African ancestor. *Nature 421*, 734–737.

Young, T.P. & Evans M.R. (1993). Alpine vertebrates of Mount Kenya, with particular notes on the rock hyrax. *Journal of the East Africa Natural History Society 82*, 55–79.

Yu, L., Li, Q.W., Ryder, O.A., & Zhang, Y.P. (2004). Phylogenetic relationships within the mammalian order Carnivora indicated by sequences of two nuclear genes. *Molecular Phylogenetics and evolution 33*, 694–705.

Zdansky, O. (1924). *Jungtertiäre Carnivoren Chinas. Palaeontologia Sinica 2*, 1–149.

Zhang, Z., & Gentry, A.W. (2002). Land mammal faunal sequence of the late Miocene of China: new evidence from Lantian, Shaanxi Province. *Vertebrata PalAsiatica 40*, 165–176.

Appendix: Endocranial morphology of the late Miocene bone-cracking hyena *Adcrocuta eximia* (Carnivora, Hyaenidae) compared with extant hyenas

Reference: Vinuesa, V., Madurell-Malapeira, J., Fortuny, J., & Alba, D.M. (2014). Endocranial morphology of the Late Miocene bone-cracking hyena *Adcrocuta eximia* (Carnivora, Hyaenidae) compared with extant hyenas. In: Arreguín-Rodriguez, G., Colmenar, J., Díaz-Berenguer, E., Galán. J., Legarda-Lisarri, A., Parrilla-Bel, J., Puértolas-Pascal, E., Silvia-Casal, R. (eds) New Insight on Ancient Life. Prensas Universitarias de Zaragoza, Zaragoza, pp 194–196.

Summary: This appendix contains the abstract of an oral communication presented in 2014 in the XII Encuentro de Jovenes Investigadores en Paleontologia (EJIP), which took place in Boltaña (Spain). The work describes and compares the brain morphology of a juvenile and an adult specimens of the Miocene hyaenid *Adcrocuta eximia.*

Author's contribution: The doctoral candidate is the first author of this work and the presenter of the oral contribution to the aforementioned meeting. He was involved in all stages of the study, including the the CT processing and 3D modeling, the description of the specimens, the statistical analyses and the writing of the manuscript.

Endocranial morphology of the Late Miocene bone-cracking hyena *Adcrocuta eximia* (Carnivora, Hyaenidae) compared with extant hyenas

Morfología endocraneal de la hyena rompedora de huesos del Mioceno Superior Adcrocuta eximia *(Carnivora, Hyaenidae) en comparación con hienas actuales*

Víctor Vinuesa[1*], Joan Madurell-Malapeira[1,2], Josep Fortuny[1] & David M. Alba[1]

[1] Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICP, Campus de la UAB s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain.

[2] Dipartimento di Scienze della Terra, Sapienza Università di Roma, Piazzale Aldo Moro 5, 00185 Roma, Italy.

* Corresponding author: victor.vinuesa@icp.cat

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Palabras clave: *Carnivora, Hyaenidae, CT-scan, encéfalo.*

Introduction

Adcrocuta eximia is the earliest recorded hyena showing fully developed bone-cracking adaptations. This successful ecomorphotype—to which three of the four extant hyenas belong—became the commonest during the Plio-Pleistocene of the Old World, as exemplified by the widely-distributed genera *Pliocrocuta* and *Pachycrocuta*. The biochronological range of *A. eximia* spans from the MN10 to the MN13, ca. 9.6-4.9 Ma (Turner *et al.* 2008). It is recorded from several Eurasian localities, mainly on the basis of fragmentary material. However, the more complete remains from the Late Miocene sites of Pikermi (Greece) and Lantian (China), given the lack of cursorial adaptations, suggest that it was a robust and powerful, but not very fast-moving, animal (Andersson & Werdelin 2005). Despite the large number of studies devoted to the external craniodental morphology of extant and extinct bone-cracking hyenas, only a few have focused on their internal cranial cavities (Joeckel 1998; Sakai *et al.* 2011; Arzsnov *et al.* 2010; Vinuesa *et al.* 2013). With the aid of computed tomography (CT) techniques, here we describe the endocranial morphology of *A. eximia*. Our study is based on two (juvenile and adult) crania from Torrent de

Traginers (MN11; early Turolian; Villalta Comella & Crusafont Pairó 1948) in the Vallès-Penedès Basin (NE Iberian Peninsula).

Morphological comparisons

Although the virtual endocast derived from the adult specimen displays some distortion, its morphology closely resembles that of the juvenile specimen, only with minimal differences in their relative proportions. Similarities relate to the main sulcal pattern (including the disposition of the cruciate sulcus, the sylvian sulcus, the ectosylvian sulcus and the suprasylvian sulcus), whereas the main difference is related to variation in length of the coronal sulcus. Similarities in brain morphology between juvenile and adult individuals had been previously reported for extant hyaenids (Arzsnov *et al.* 2010), suggesting that no significant changes occur in this regard throughout postnatal ontogeny.

When compared with the endocranial morphology of the four extant hyaenids, the studied fossil endocasts show many similarities, including a similar disposition and length of the sylvian, suprasylvian and ectolateral sulci. In contrast, *A. eximia* remarkably differs from all of its extant counterparts in the position of the cruciate sulcus. This feature is important, because the position of this sulcus (and, thus, the development of the frontal cortex) is correlated with sociality among extant hyaenids (Holekamp *et al.* 2007; Sakai *et al.* 2011). In *A. eximia*, this sulcus is situated more anteriorly than in extant bone-cracking hyenas, thus more closely approaching the condition of the insectivorous *Proteles*. This similarity between *A. eximia* and *Proteles* suggests that the former displays a more primitive endocranial morphology than its extant ecomorphological analogs. Given that *A. eximia* is customarily related to the extant spotted hyena (*Crocuta crocuta*) based on external craniodental characters (Turner *et al.* 2008), the observed endocranial similarities with *Proteles* are probably indicative of a less elaborated social behavior compared to extant bone-cracking hyenas.

The preliminary work reported here represents a first step for the study of the endocranial morphology of *A. eximia*. More refine morphometric and statistical comparisons between this taxon and extant bone-bracking hyenas will hopefully provide a better understanding of the evolution of hyaenid cognitive abilities in relation to social behavior, diet and locomotion.

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REFERENCES

Andersson, K. & Werdelin, L. (2005). Carnivora from the Late Miocene of Lantian, China. *Vertebrata PalAsiatica*, 43, 256-271.

Arsznov, B.M., Lundrigan, B.L., Holekamp, K.L. & Sakai, S.T. (2010). Sex and the frontal cortex: A developmental CT study in the spotted hyena. *Brain, Behavior and Evolution*, 76, 185-197.

Holejamp, K.E., Sakai, T.S. & Lundrigan, B.L. (2007) Social intelligence in the spotted hyena (*Crocuta crocuta*). *Philosophical Transactions of the Royal Society B*, 362, 523-538.

Joeckel, R.M. (1998). Unique frontal sinuses in fossil and living Hyaenidae (Mammalia, Carnivora): description and interpretation. *Journal of Vertebrate Paleontology*, 18, 627-639.

Sakai, S.T., Arsznov, B.M., Lundrigan, B.L. & Holekamp, K.E. (2011). Brain size and social complexity: A computed tomography study in Hyaenidae. *Brain, Behavior and Evolution*, 77, 91-104.

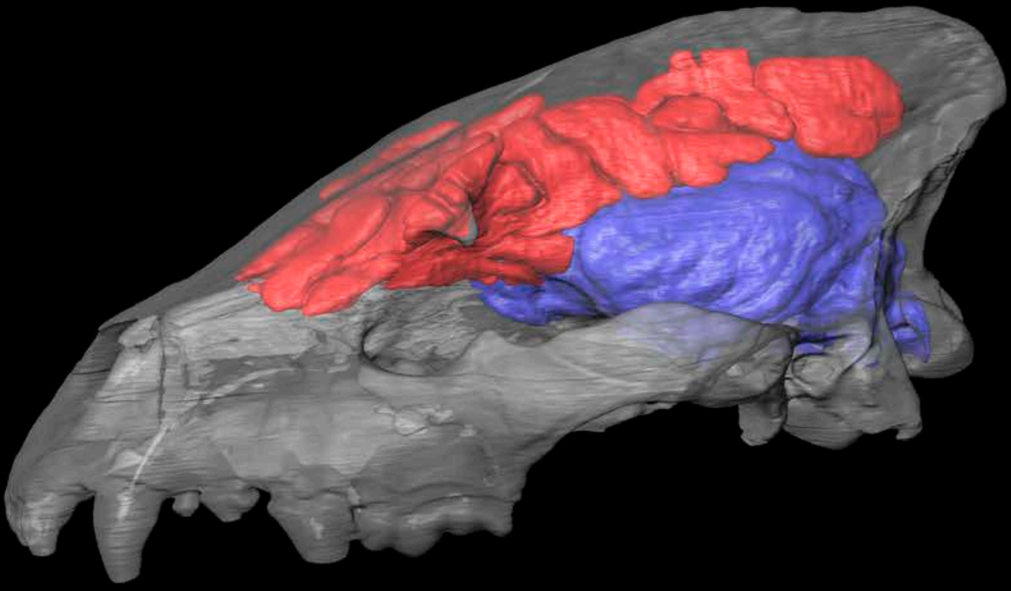
Turner, A., Antón, M. & Werdelin, L. (2008). Taxonomy and evolutionary patterns in the fossil Hyaenidae of Europe. *Geobios*, 41, 677-687.

Villalta Comella, J.F. de & Crusafont Pairó, M. (1948). Nuevas aportaciones al conocimiento de los carnívoros pontienses del Vallés-Penedés. *Publicaciones del Instituto Geológico, Diputación Provincial de Barcelona*, 7, 81–121.

Vinuesa, V., Madurell-Malapeira, J., Fortuny, J. & Alba, D.M. (2103). The internal cranial morphology of the extinct bone cracking hyena *Pliocrocuta perrieri* (Carnivora, Hyaenidae). *Journal of Vertebrate Paleontology*, 33(1), 232-233.

Institut Català de Paleontologia
Miquel Crusafont

Departament de Geologia de la
Universitat Autònoma de Barcelona



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