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Dance of the Cave Bear: Honouring the Scientific Legacy of Björn Kurtén

The hyena story: from ancient fossils to folktales and witchcraft

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Hyaenidae is a carnivore family with only four extant species, yet a diverse and abundant presence in the fossil record. Today's generalized antagonistic attitudes towards hyenas may be the product of entangled hyena–hominin geographies since the origin of humanity. These shaped ecocultural relationships and may well have affected the convergent evolution of salient traits like complex social systems. In fact, spotted hyenas have been proposed as models of early human evolution. Björn Kurtén had a great interest in fossil hyenas as study objects, having written several publications on this group, including pioneering and comprehensive studies that laid the foundation for major works to follow. Thus, in tribute to Björn Kurtén, we provide an encapsulated overview of his contributions and review recent developments in the understanding of Hyaenidae evolution and ecologies. We conclude with a synopsis of hyenid and hominid interactions from ecological, evolutionary and cultural perspectives.

Introduction

Today, Hyaenidae is a small carnivore family with only four extant species: the spotted hyena (*Crocuta crocuta*), the brown hyena (*Parahyaena brunnea)*, the striped hyena (*Hyaena hyaena*) and the aardwolf (*Proteles cristatus)*. In the fossil record, however, hyenids exhibit both diversity and abundance. Hyaenidae originated in Eurasia about 25 million years ago, reaching a peak of diversity in the Late Miocene. Over 80 species of hyenids have been described (Werdelin & Solounias 1991). Three of the four extant species are exclusively found on the African continent, and only one of the extant species retains a part of its range in Asia (Wilkinson *et al.* 2024). Taxonomic challenges have hampered the study of this group, but methodological developments, particularly during the last two decades, have allowed new insights into the evolution of the lineage. Despite the reduced number of species extant today, a

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substantial diversity of ecologies persists, with hyenids covering important ecological niches. Unfortunately, according to the IUCN, two of these extant species are rare and near-threatened (AbiSaid & Dloniak 2015, Wiesel 2015). With human–hyena conflicts increasing globally as a result of human population growth and wild prey declines, their threat status is expected to worsen. Hyenas and hominins have long interacted, and although hunter and scavenger roles during the Pleistocene are still disputed, recent studies are broadening the understanding of hominin–hyenid interactions and co-evolution, moving beyond the purely antagonistic views centered on competition and conflict through more complex ecocultural perspectives.

In the following, we provide a brief overview of the evolution of hyenids through the prism of Björn Kurtén's contributions, present updated insights for extant hyenas, and conclude with reflections on hominin–hyenid interactions from the Pleistocene to present, with particular emphasis on hyenids in hominin culture.

From Kurten's contributions to current understanding of Hyaenidae evolution

Hyaenidae originated in Eurasia during the Early Miocene, with viverrid- and herpestid-like basal forms like the oldest identified hyenid *Protictitherium* (Werdelin & Solounias 1991). The fossil record for hyenids is diverse, with over 80 species described. Both taxonomic and functional diversity grew gradually during the Miocene, peaking in the Late Miocene with 24 species. It is during the Middle Miocene that hyenids reached Africa (Werdelin & Peigné 2010). Although the evolution of the group was initially gradual, including a large number of jackal-sized forms, in the Late Miocene, two radiations have been identified, one including wolf-like cursorial hyenids, and the other leading to the large bone-cracking forms of the Plio-Pleistocene. The composition of the family changed over time in size, morphology and ecological niche (Werdelin & Solounias 1991, Turner *et al.* 2008), with six ecomorphs recognized: civet-like insectivore/omnivores, mongoose-like insectivore/omnivores, jackal- and wolf-like meat and bone eaters, cursorial meat and bone eaters, transitional bone crackers and fully developed bone crackers. Details of the evolution of these different ecological groups are still being worked out, as is the biogeography of some major taxa. Nonetheless, transitional bone crackers and fully developed bone-cracker hyenids have independently arisen on at least two occasions (Coca-Ortega & Pérez-Claros 2019).

The family saw important diversity declines immediately after the Late Miocene diversity peak and then later during the Early Pleistocene. During the first downturn, it was particularly the canid-like morphotypes that declined, coinciding with the appearance, expansion, and diversification of canids in Eurasia. Except for the aardwolf, this group of 'non-hyenids' (*sensu* Werdelin & Solounias 1991) is now extinct. Instead, the 'hyenid-like' taxa peaked in diversity later, surviving the expansion of canids in Eurasia and becoming the dominant scavengers of Eurasia in the Pliocene.

Björn Kurtén's works encompassed most of the evolutionary span of the Hyaenidae family (Werdelin 1992). His contributions extend from the study of Miocene canid-like hyenid radiations, through comprehensive work directed at resolving the taxonomic pandemonium of Plio-Pleistocene hyenids, to examinations of cave hyena (*Crocuta spelaea*) temporal and spatial morphometric variation from Pleistocene to Holocene. Some of his contributions to the field were seminal and are still relevant today, others inspired new lines of research. He described three hyenid species that retain validity today (Werdelin & Solounias 1991).

Kurtén's major contributions to the study of hyenas came early in his career with his seminal study of the Chinese Late Miocene '*Hipparion*' fauna (Kurten 1952). The carnivore element in this fauna is dominated by hyenas and could be said to form the pinnacle of success of the Hyaenidae, with numerous forms ranging from jackal- to wolf-sized, and including a single genus, *Adcrocuta*, that presaged the living hyenas in its adaptations to scavenging. This fauna had previously been studied by Zdansky (1924), yet Kurtén brought it to new life. For his thesis (Kurtén 1953), Kurtén continued the *Hipparion* fauna work, although focusing on the ictithere (canid-like) hyenas as a cornerstone of his study on population dynamics of fossil mammals. Because these hyenas had definable wear stages in their cheek dentition, Kurtén was able to construct age pyramids for these animals and thereby investigate their population structure. He followed this up with a study specifically of the ictitheres and their radiation (Kurtén 1954). This pioneering work was subsequently continued by several authors in numerous works (Kurtén 1985, Qiu 1985, Werdelin 1988, Semenov 1989, Werdelin & Solounias 1991), becoming a cornerstone of the study on faunal, especially carnivore, dynamics in the Late Miocene of Eurasia.

Later, Kurtén (1956) turned his attention to hyenas of the Pliocene and Pleistocene and sorted out a considerable degree of confusion regarding the taxonomy of these hyenas. In doing this he laid the foundation for the study of Plio-Pleistocene hyenas today. The following year Kurtén (1957a) tackled an issue that is still at the forefront of research on fossil hyenas: the ‘percrocutoid’ problem.

In the same year Kurtén also published a brief paper that addressed size fluctuations in bears and hyenas (specifically *Crocuta spelaea*) during glacial-interglacial cycles in Europe (Kurtén 1957b). This idea was subsequently fully developed and investigated by Klein and Scott (1989). In this same paper, he paid attention to the size cline connecting extinct and extant *Crocuta*, initially suggesting such size differences should not suffice for subspecific status of the extinct cave hyenas. However, in a follow-up paper (Kurtén 1968), he supports the allocation to *Crocuta crocuta spelaea* based on differences in the metapodials.

Work by Kurtén on hyenas in the 1960s and 1970s mostly involved descriptions of material from specific sites. Prominent among these is the material from Petralona (Kurtén & Poulianos 1977, 1981) which is very extensive. In the 1980s, Kurtén returned to his early work on ictitheres with an important paper (Kurtén 1982) showing definitively the difference between *Ictitherium viverrinum* and *Thalassictis robusta* and their respective descendants. These are two of the most common hyenid genera of the Late Miocene, together with *Hyaenictitherium* (a descendant of *Thalassictis*). The confusion between these two genera had plagued hyena studies since the 1950s and was finally resolved in Kurtén (1982). He followed this up (Kurtén 1985) with a return to the subject of his 1954 paper on the ictitheres. Lastly, he published a paper on the aberrant genus *Chasmaporthetes*, the only hyena to reach North America (Kurtén & Werdelin 1988). That paper remains a central reference for the study of this genus.

Kurtén’s thorough work with meticulous attention to detail, visionary approach, and innovative methods, despite the technical limitations of his time, are noteworthy. Some of the topics he addressed are still at the frontline of hyenid research. However, recent methodological advances, such as X-ray computed tomography and 3D-laser scanning combined with machine learning, paleogenomics through improved methods for the extraction of ancient DNA, and the development of comprehensive fossil databases, are rapidly advancing the field and shaking up some of the older theories (Uhen *et al.* 2013, Arriaza *et al.* 2019, Courtenay *et al.* 2021, Žliobaitė *et al.* 2023, Abdelhady *et al.* 2024, Westbury *et al.* 2024). The following sections give the flavor of Kurten’s legacy in selected fields of hyenid research.

The percrocutoid problem

The ‘percrocutoids’ are a seemingly precocious hyenoid offshoot first described from India and China in the beginning of the 20th century. The earliest described percrocutoids were large and rather *Crocuta*-like and therefore described as species of that genus, following the general trend of the time to assign all large fossil hyenids to extant genera. In his wholesale revision of hyenid taxonomy, Kretzoi (1938) coined the genus *Percrocuta* for one of the then known species. This was not followed by other scientists of the time, however, and it was not until Kurtén’s work (Kurtén 1957a), that *Percrocuta* (although as a subgenus) arrived in the general consciousness. Several genera and species have been named since then.

‘Percrocutoids’ originated in the early Middle Miocene, probably in China. The earliest were larger and had more durophagous dentitions than other hyenids known from that time. This, together with some morphological features, such as a deciduous carnassial that differs in structure from that of hyenids (Guanfang & Schmidt-Kittler 1983), led to the transfer of ‘percrocutoids’ from Hyaenidae to a family of their own, Percrocutidae. Recently, however, the first basicrania of percrocutoids have been retrieved (Xiong 2019, 2022). These are of general hyenid character and therefore ‘percrocutoids’ have been reintroduced into Hyaenidae as a subfamily, Percrocutinae. Despite this, the ‘percrocutoid problem’ remains. Even if we were to agree that they belong to Hyaenidae as a subfamily, the new problem becomes how to identify members of this subfamily because there are no clear morphological characters that distinguish them. Identifying and characterizing members of Percrocutinae now becomes a new research frontier, one begun by Björn Kurtén when he took up the gauntlet thrown down by Miklos Kretzoi when the latter, largely on instinct, coined the genus *Percrocuta*.

The Miocene: heyday of hyenas

One part of the paleontological legacy available in Helsinki when Björn Kurtén started his career was the collections of his predecessor Alexander von Nordmann. These collections were gathered in the Black Sea region of what is today Ukraine, and included both Pleistocene and Miocene fossils. Among the fossils was a small, Miocene hyena that von Nordmann named *Thalassictis robusta.* This is one of the first described canid-like hyenas of the Miocene and led to a life-long interest in these animals on the part of Kurtén. As early as 1954, Kurtén described the von Nordmann collection of Miocene hyenas in Helsinki. Thirty years later he returned to this topic by clarifying the distinction between von Nordmann’s *Thalassictis* and *Ictitherium*, described a few years later. This work catalyzed subsequent work by one of us (Lars Werdelin) and colleagues from Ukraine and China to further understand the radiation of hyenas into dog-like niches in the canid-free Eurasian Miocene, leaving Hyaenidae as the best studied carnivore family in Eurasia (Qiu 1985, 1987, Semenov 1989).

Paleogenomics of hyenas

The genus *Crocuta* was one of the most widespread carnivore taxa in the Plio-Pleistocene, with a range that encompassed essentially all of Eurasia and Africa, although, unlike its contemporary the African lion (*Panthera leo*), it never crossed the Bering Strait. This wide range and abundance of material has interested specialists for decades and Björn Kurtén was no exception, penning several papers on the genus. He was especially interested in the ‘cave’ hyenas of western Eurasia (*Crocuta spelaea*) which he considered distinct from the modern species. He did not live to experience the genomic revolution, but he would certainly have been interested in the emerging results from the paleogenomic studies of the genus. Several papers detailing this have been recently published (Rohland *et al.* 2005, Sheng *et al.* 2014, Rao *et al.* 2020, Westbury *et al.* 2020, 2021). The current view is that ancestral cave hyenas separated from the modern species in the Early Pleistocene, migrating from East Africa to eastern Asia and then west into Europe in the Middle Pleistocene, where they replaced hyenas of the *Pachycrocuta* lineage. Subsequent admixture of *C. spelaea* with *C. crocuta* from Africa, possibly in the Levant, suggests a process similar to that which led to admixture between modern humans and Neanderthals (Lalueza-Fox & Gilbert 2011, Simonti *et al.* 2016, Quilodrán *et al.* 2024, Westbury *et al.* 2024).

The extant hyenids: who, where and how

For Kurtén, studying the living organism was important to understand their fossil counterparts (Anderson 1991). Despite the Eurasian origin of Hyaenidae, all extant species are thought to have originated in Africa, where they retain their distributions today (Fig. 1). Two of the four extant taxa, or their immediate ancestors, colonized Eurasia from Africa: *Crocuta* and *Hyaena.* The spotted hyena had its broadest distribution during the Late Pleistocene (Kurtén 1968), covering much of Eurasia from Iberia through Europe to the Pacific coast of the Russian Far East (*see* also Fig. 2), with the Urals being

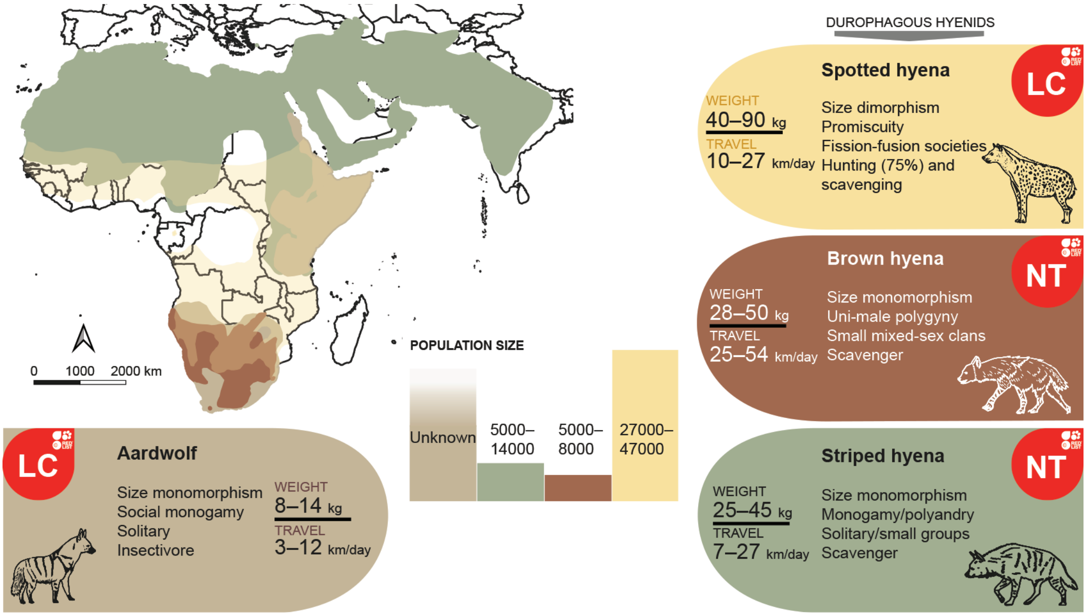

Fig. 1. Distribution (map), estimated population sizes (bar graph), diet preferences, social organization characteristics and threat status (Red List icons: LC = Least Concern, NT = Near Threatened) of the four extant hyenids (three durophagous species on the right, myrmecophagous species on the left).

the northernmost location (Kahlke 1999). They became regionally extinct from central Europe at 40 000 years ago (ka), retaining only warmer south-western European localities and disappearing completely from the continent before 30 ka (Stuart & Lister 2014), coinciding with the decrease in grasslands and gradual increase in mixed woodlands, where wolves, and humans, had advantage (Stiner 2004).

Hyaena hyaena is not known as a fossil outside Africa. Thus, we know much less of the biogeography of the species and how or when it dispersed to Asia. The evolution and biogeography of *Parahyaena brunnea*'s lineage is also unclear, but it seemingly did not leave Africa, with fossils known with certainty only from South Africa, and a tentative record in Kenya (Werdelin & Barthelme 1997). No fossils of *P. brunnea* have conclusively been allocated to European sites (but *see* Pérez-Claros 2024). At present, the striped hyena has the largest geographic distribution, still occurring in Asia, extending from northern Africa through the Arabia Peninsula to India (Fig. 1). The aardwolf lineage separated from the other extant hyena species 13 million years ago (Ma), coinciding with the first appearance of hyenids in Africa and thus supporting an African origin for the four species we have today (Westbury *et al.* 2019).

Westbury *et al.* (2021) estimated effective population sizes of the four extant hyena species from 2 Ma to present based on their genetic diversity, showing that the aardwolf has kept the largest populations, followed by spotted hyena, throughout the entire period. The two species have had similar population histories despite their very different ecologies: a slow decrease in population size from 1.5 Ma, a rapid recovery at about 500 ka, and a plummeting decrease at about 100 ka; this decline at 100 ka is shared by the other two, rarer hyena species, and parallels observed declines for ruminants (Chen *et al.* 2019). These genetically inferred population estimates align well with independent population estimates for the four species (Fig. 1).

The Hyaenidae family exhibits a diverse range of social structures, from solitary to highly gregarious (Wagner 2006, Watts & Holekamp 2007, Holekamp & Sawdy 2019) as well as a diversity of feeding strategies and diets (Fig. 1). Spotted hyenas are cursorial hunters that feed mostly on mid- to large-sized live herbivores; striped

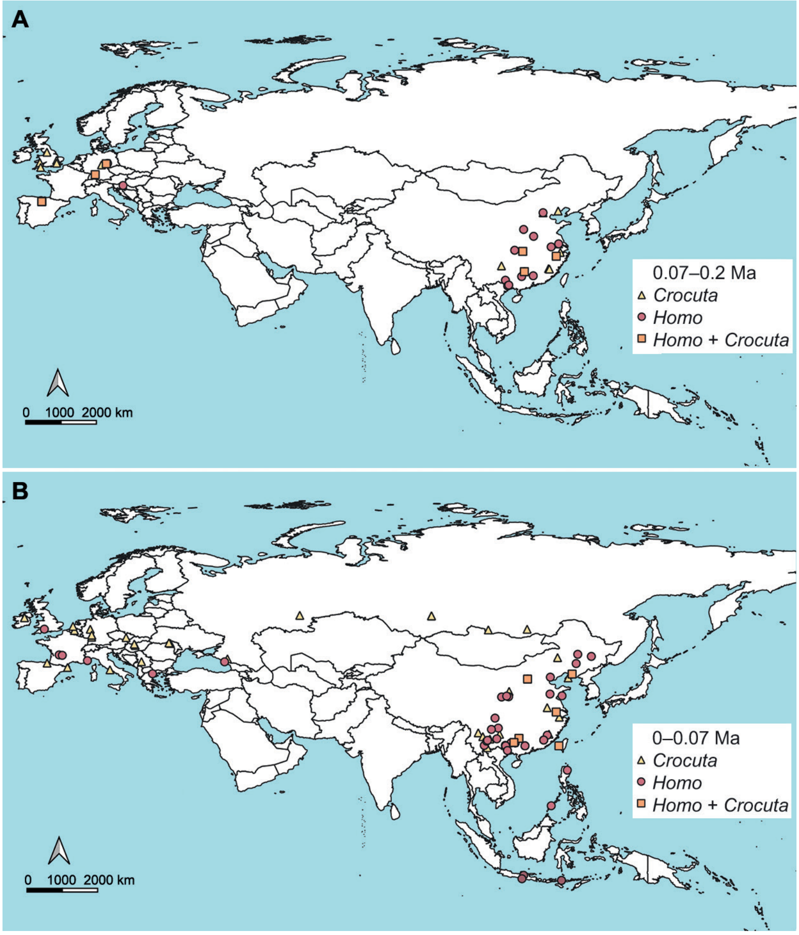

Fig. 2. *Crocuta* and *Homo* fossil localities, dated to (**A**) 0.07–0.2 Ma, and (**B**) 0–0.07 Ma. Only Eurasian fossil records are shown. *Crocuta* and *Homo* were queried from the open access NOW database, filtered for the selected period, accepting only the localities with dating and rejecting general localities, which may present several separate fossil accumulations/localities. Coordinates for localities were extracted and those with presence of *Crocuta*, *Homo* or both, are shown on the map.

and brown hyenas are predominantly scavengers, complementing their diets with fruits and insects. The aardwolf instead, is an insectivore specialized in termites. The three durophagous species (*C. crocuta, P. brunnea and H. hyaena*) present different degrees of matrilineal social organization. Spotted hyenas exhibit the most complex societies, reminiscent of cercopithecine primates (Holekamp *et al.* 2012). Brown hyenas display intermediate levels of sociality with small mixed-sex clans and striped hyenas and aardwolves are predominantly solitary (Holekamp & Sawdy 2019) although some level of sociality is reported for striped hyenas (Tichon *et al.* 2020). Some form of gregariousness has been observed nonetheless in the two scavenging species when resources abound (e.g. Califf *et al.* 2020). The inclination towards sociality in hyenas likely arose from the necessity to secure food resources from competitors and not as a response to predation pressure (Watts & Holekamp 2007, Holekamp & Sawdy 2019). Remarkably, all the hyena species, including the spotted hyena, forage predominantly solitarily, and thus cooperative hunting is not viewed as a likely factor in the evolution of sociality in the group. For striped and brown hyenas, specialization in carrion means reliance on a scarce, patchily distributed, and unpredictable resource that cannot be shared and does not support large populations. This results in less direct competition at carcasses with conspecifics, yet territories are defended (Wagner 2006). Instead, spotted hyenas, with diets dominated by hunted mid- to large-sized herbivores, rely on abundant and more spatially predictable resources that often can support larger populations, yet facing scramble competition. Spotted hyenas often inhabit and forage in environments where competitors like African lions and members of neighboring hyena clans can readily detect kills, which are typically too substantial to be monopolized by a single individual. Sociality in spotted hyenas thus may have evolved in response to the need of defending such food resources (Watts & Holekamp 2007), leading females to form clans to safeguard food sources and protect territories in regions of elevated population density (Holekamp & Sawdy 2019).

The evolution of sociality is difficult to separate from that of diet and specialized dentition, and where some of the species exhibit sociality particularly to defend food resources, others show sociality when caring for the young. Spotted hyenas have developed a dentition that favors rapid tearing and ingestion of fresh meat and bones at rates of up to 1.3 kg per minute (Smith & Holekamp 2023). Such fast rates, in combination with a solitary hunting strategy, allow those individuals that perform the hunt to take in the equivalent of daily energy requirements before competitors arrive and resources are shared (Holekamp *et al.* 1997). Solitary scavengers like the striped and brown hyenas cannot compete in feeding speed nor with numbers of conspecific feeders at carcasses. To successfully feed in areas where they coexist with spotted hyenas, they thus tend to adjust their daily activity, often displaying broader temporal activity patterns than spotted hyenas (Schuette *et al.* 2013, Vissia *et al.* 2021). When finding carcasses at times when spotted hyenas are not active, they feed partially *in situ* but then transport parts of the carcass to the dens. In fact, the two scavenging hyenas display somewhat different denning behavior than the hunting spotted hyena and also have larger litter sizes. All three species supplement suckling by provisioning their cubs with meat and bones, although this happens more frequently for striped and brown hyenas (Holekamp & Smale 1990) and they often transport food items over longer distances, i.e., tens of kilometers (e.g. Skinner 2006). Also, both parents and older siblings may provision den-dwelling cubs in the two scavenging species, while only the mother does this in spotted hyenas. Pérez-Claros and Coca-Ortega (2020), noting that scavenging hyenids have larger canines in relation to carnassials, as opposed to hunting hyenids, suggest that such large canines, particularly the lower ones, would have developed to favor the transportation of carcasses to the dens. On the other hand, the scavenging hyenas also display spatial niche segregation from the hunting hyenas, although both the striped and the brown hyena have regionally overlapping distributions with the spotted hyena. In general, brown and striped hyenas are excluded from the most productive areas, coexisting with spotted hyenas only at locations with low prey availability where densities of spotted hyenas are low (Schuette *et al.* 2013, Williams *et al.* 2021, but *see* Vissia *et al.* 2021).

The origins of sociality in hyenids are still disputed. Inferring sociality from ancestral lines of extant hyenids is not straightforward, however both dentition and brain size have been used as proxies. For instance, the relative development of the anterior area of the brain (anterior cortex), which appears to correlate with sociality across the extant hyenids, would indicate that the Late Pliocene *P. perrieri* (Vinuesa *et al.* 2015) and the *C. spelaea* and *C. ultima* of Eurasian Pleistocene (Vinuesa *et al.* 2016) had reduced social abilities, with brain proportions more similar to those of *Hyaena* and *Parahyaena.* The greater development of the anterior cortex in extant *C. crocuta* from Africa would thus be a more recent evolutionary acquisition. Nonetheless, the relationship between forebrain and sociality is still questioned and an area of ongoing research. On the other hand, Pérez-Carlos and Coca-Ortega (2020), by looking at the relative size of canines and carnassials, suggest that the large canines of *P. brevirostis* would position it as a solitary scavenger transporting bones to the den. Similar dentition is observed in the scavenging *P. perrieri*. However, such a model is less clear for *C. spelaea*, for which some indicators (brain size, bone accumulations) would suggest a solitary scavenging behavior, but its dentition corresponds more to that of the hunting spotted hyena.

Both scavenging habits and sociality result in high pathogenic risks and can thus explain the selection pressure on the immune system of the durophagous hyenids. Indeed, all the extant hyenid species exhibit high diversity in the Major Histocompatibility Complex (MHC) (Heinrich *et al.* 2016, Califf *et al.* 2020), higher than other carnivores including felids like leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*) (Heinrich *et al.* 2016). Although some divergence in MHC between striped and spotted hyena exist, shared aspects are explained through a common carrion feeding ancestor facing strong selection for pathogen resistance (Shao *et al.* 2022).

Nevertheless, despite the accumulating knowledge of extant hyenids, this taxonomic group has not received as much research attention as other carnivore groups such as canids and felids. Important taxonomic, geographic and topical research biases have recently been identified (Wilkinson *et al.* 2024), highlighting that the ecology, distribution and population status of aardwolf and striped hyena remain largely understudied. The elusive and solitary behavior of these two species indeed challenges their study. Nonetheless, methodological advances in ecological research are rapidly boosting our understanding. In particular, camera-trapping studies are proliferating, with applications found for the four species, targeting estimations of population abundances, diel activity, niche partitioning and social interactions (Dheer *et al.* 2022). The rapidly increasing uptake of biologging technologies has also reached hyenid research, especially through the deployment of biologgers on spotted hyenas in well-established long-term projects. These tools are facilitating better understanding of the details of social interactions as well as of hyena biomechanics (Minasandra *et al.* 2023, Strauss *et al.* 2024). Radiotracking, or movement studies of the three other species are still lacking, though, and similarly rare are applications of metagenomics to study hyenid diets, in contrast with the abundant applications for many other large carnivores. In fact, much of the current knowledge on hyenid diets comes from classic studies (*see* e.g. Kruuk 1972, 1976, Kruuk & Sands 1972) and anecdotal evidence that do not cover well the diversity of ecosystems and carnivore communities these species live in today. A further concern is the lack of understanding of hyena–human interactions (Wilkinson *et al*. 2024).

Hominins and Hyaenidae, friends or foes

Today, one of the keys for the survival of hyenas is their ability to adapt to the human modified landscape. In Africa, hominins and hyenas have shared spaces since the Pliocene (Werdelin & Lewis 2005). Interactions with hyenas and other large carnivores are viewed as critical in early hominid evolution (Stiner 2012). These interactions may have shaped hyena evolution as well, but this perspective has been seldom addressed (Hussain 2023). Humans and the modern spotted hyena show convergent evolution, both exhibiting complex social structures and behavioral plasticity. Smith *et al.* (2012) have even suggested that spotted hyenas are a valid model for human evolution that can help us understand our past.

Existing evidence demonstrates that hyenas were present in ancestral human landscapes throughout human evolution (Werdelin & Lewis 2005). Early on, hominins were predominantly prey to hyenas. This may have even resulted in the scarcity of hominin fossils as the hyenas crushed and digested their prey (Baynes-Rock 2015a). Some evidence escaped the carnivore jaws, such as few *Ardipithecus* remains from Ethiopia (White *et al.* 2009). Although the carnivores at the site have yet to be described, the coexistence of those early hominins with ancestors of the extant striped and spotted hyenas, is highly probable (Louchart *et al.* 2009). Also, *Australopithecus anamensis* in Kenya, and *Australopithecus afarensis* in Tanzania, shared landscapes with at least four hyenids (Werdelin & Lewis 2005, 2020, Werdelin & Dehghani 2011). Indeed, hominin fossils often exhibit hyena tooth marks (Baynes-Rock 2015a).

In the Pleistocene, hominins went from being hunted to becoming the hunters. Hominins of the Pliocene had predominantly herbivorous diets, but at 3–2 Ma, the development of tools facilitated the consumption of meat (Lee-Thorp *et al*. 2000, Domínguez-Rodrigo & Pickering 2017, Ben-Dor *et al.* 2021) and the hunting of prey larger than the hominids themselves. Compiling a comprehensive and diverse set of evidence, Ben-Dor *et al.* (2021) showed that the trophic level of the *Homo* lineage evolved from a low base to a high carnivorous position during the Pleistocene, beginning with *Homo habilis* and peaking in *Homo erectus*. This led to novel interactions between hominins and carnivores,

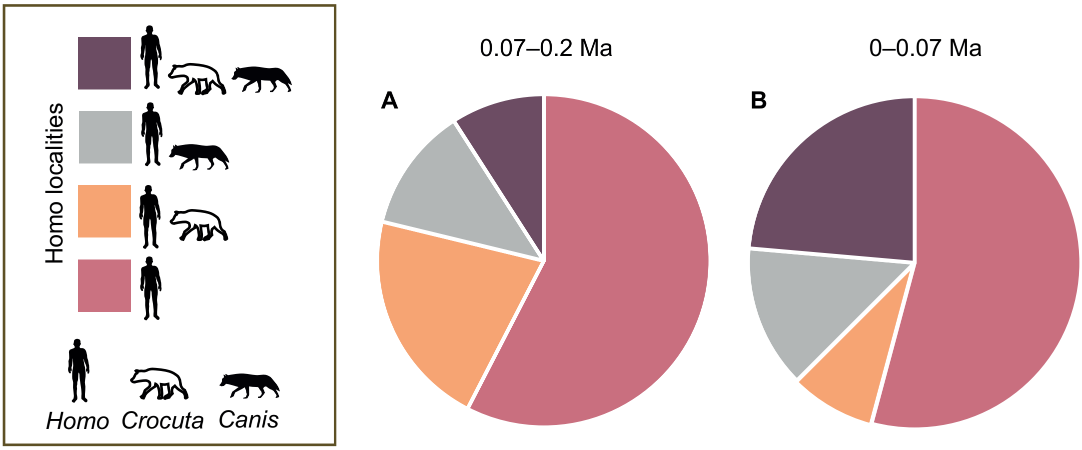

Fig. 3. Fraction of *Homo* fossil localities shared with *Crocuta*, *Canis* and both species for the period of anatomically (**A**) archaic humans (0.07–0.2 Ma) and (**B**) modern humans (0–0.07 Ma), at 33 and 72 *Homo* fossil localities, respectively. For these same periods (0.07–0.2 Ma and 0–0.07 Ma) there are 36 and 106 localities with *Crocuta* fossils, and 35 and 215 localities with *Canis* fossils, respectively.

hominins entering the hypercarnivore guild, and becoming competitors in a diverse assemblage (Lewis & Werdelin 2007, Werdelin & Lewis 2013). The hunting-scavenging debate, or whether early hominins accessed meat through hunting, aggressive scavenging or passive scavenging is by no means resolved, and certainly important for understanding hominin–hyenid interactions during the time.

Hyenids, together with other carnivorans, are considered to have either fostered, or hampered the success of the early hominin dispersals beyond Africa (Mateos *et al.* 2024). Most scholars argue that the large carnivore guild enabled the success of early humans, and it was the interactions in the hypercarnivore guild that facilitated the spread of the first *Homo* sp. to Eurasia in the Mid-Pleistocene (Arribas & Palmqvist 1999). The genus *Crocuta*, having evolved in Africa, had spread to Eurasia before the early humans (Stuart and Lister 2014, Westbury *et al.* 2020). The genus persisted until the Late Pleistocene surviving the larger *Pachycrocuta*, with some of the Pleistocene localities recording the two bone-crushing hyena taxa (Lewis & Werdelin 2022). Both humans and *Crocuta* resisted the climatic fluctuations of Eurasia in the late Pleistocene, flourishing while many other carnivores disappeared (Stuart & Lister 2014, Varela *et al.* 2015, Timmermann & Friedrich 2016).

For illustrative purposes, here we examine records of Late Pleistocene fossil localities extracted from the NOW database of fossil mammals (NOW Database of fossil mammals, https://doi.org/10.5281/zenodo.4268068, Žliobaite *et al.* 2023) for two time periods (0–0.07 and 0.07–0.2 Ma) corresponding to before and after the arrival of anatomically modern humans (ca. 70 000 bp). *Homo* and *Crocuta* in Eurasia seem to share similar biogeographies (Fig. 2), although *Crocuta* appears to be more broadly distributed, with more localities, particularly in central Asia for the modern period, and in southeastern and northwestern Europe for the period of archaic humans. We further look at the overlap between *Homo* and *Crocuta* fossil localities, considering also the occurrence of wolf-like *Canis* (*C. mosbachensis*, *C. lupus*) (Fig. 3). Canids escaped the megafaunal extinctions of the Pleistocene, and they have often been considered as humanity's fellow traveler in the period, with their interspecific interactions leading to the domestication of the dog at the end of the Pleistocene ca. 15 000 bp (O'Regan *et al.* 2011, Freedman *et al.* 2014, Timmermann & Friedrich 2016). The data available in the NOW database indicate that at least earlier on, it may have been the spotted hyena that was more closely associated with humans (Fig. 3; *see* also Stiner, 2002). In fact, *Crocuta* was present in about 30% of the

Homo localities during both periods, but in the more modern period (0–0.07 Ma), 80% of these shared localities were also shared with *Canis* and the fraction of localities shared between *Homo* and *Canis* increased during that period from 21% to 34%. Overall, these results support the persistence and expansion of canids during the Late Pleistocene, surviving the Last Glacial Maximum, whereas *Crocuta* became extinct from Eurasia. Nonetheless, while the three taxa may have shared the same landscapes, the degree to which they interacted is less clear. Some evidence from Late Pleistocene Italy suggests that wolves preferred more woodland and highland prey species, while spotted hyenas and humans shared a preference for more open habitats and, to some extent, similar prey, thus supporting some geographical separation of canids from *Homo–Crocuta* localities (Stiner 2004).

Neanderthals (and other archaic northern humans) were big-game hunters that not only shared the landscapes with *Crocuta* but also shared the same caves and other shelters, probably in temporal succession. And although this may have meant competition, it has been argued that the partial consumption of carcasses by Neanderthals and early humans may have also facilitated more abundance and predictability of resources for hyenas, once hominins became effective hunters of larger prey (as large as straight-tusk elephants; Konidaris & Tourloukis 2021, Gaudzinski-Windheuser *et al.* 2023, 2024), and more selective with the prey parts that would be consumed (Patou-Mathis 2000). Like modern humans, and unlike *Crocuta*, they probably were not able to use protein as the only source of energy but needed more fatty parts of the carcass (Speth & Spielmann 1983, Lahtinen *et al.* 2021). Despite preferring similar environments, their consumed prey or prey parts appear to differ, whether due to niche partitioning, an outcome of hunting ability linked to the development of projectile hunting (Orbach & Yeshurun 2021), or a group-size effect, with larger groups hunting larger prey (Périquet *et al.* 2015). In any case, our exploratory exercise supports the idea of *Crocuta* and humans as fellow travelers, at least in Late Pleistocene Eurasia. But this coexistence in Eurasia did not last until the present. The cause of the eventual extinction of *Crocuta* from the continent and what role humans played in that extinction remain unclear. The climatic change, with consequent development of more forested landscapes in the north was probably an important driver, but the direct and indirect competition with humans, and potentially *Canis*, combined with decreasing prey availability may have eventually extirpated *Crocuta* populations from Eurasia (Varela *et al.* 2010).

Nevertheless, the two taxa were geographically close over long periods of time, providing an opportunity to not only co-evolve, but also to affect each other's cultures substantially. Remarkably, Pleistocene hominin–hyena interactions have predominantly been addressed from ecological and evolutionary perspectives, lacking a socio-cultural view. The emerging field of multispecies studies though, has recently turned attention to the phenomenological implications of living with carnivores, such as hyenas, leading to calls for viewing Pleistocene carnivores as key actors in the cognitive worlds in which past hominins operated and where our eco-culture evolved (Baynes-Rock 2015a, Hussain *et al.* 2022). Along these lines, Hussain *et al.* (2022) view the entanglement of hyena and Neanderthal geographies not only as spatial co-occurrence but also as socioecological proximity, with hyenas becoming an integral part of Neanderthal society and culture. Neanderthals would have developed interest in acquiring hyena-related knowledge, with hyenas becoming prominent in Neanderthal social memory through processes of landscape learning (Rockman 2009).

It may at first be perplexing that such intertwined relations are rarely depicted in Paleolithic rock art, as opposed to the more notable appearance of other large and fierce carnivores (Spassov & Stoytchev 2004, 2005). It has been argued that socio-psychological factors can help explain such absence, with hyenas being mundane, less worthy of worship than rarer but dangerous enemies or desired prey. Interestingly, humans also rarely appear in cave art. Nevertheless, the daily coexistence and competition, and perhaps also the realized resemblance in many behavioral aspects to humans, led hyenas to be despised by many societies (Glickman 1995, Hugosson 2021, Small 2021). Dislike for hyenas is ever present in written history, from Greek times through medieval ages, to today's disdain also in societies where hyenas are not encountered. Even Roosevelt and Hemingway wrote substantial derogatory passages about spotted hyenas (Roosevelt & Heller 1914, Hemingway 1935), raising and perpetuating many of the myths that contribute to their reputation, including hermaphroditism, scavenging behavior and cowardice. Interestingly, Aristotle and Pliny the Elder attempted to dismiss some of these myths that were persistent already in antiquity (Glickman 1995). It is unclear, though, whether they were referring to the striped hyena rather than the spotted hyena, which is the one that carries most of the blame. The bestiaries of the Middle Ages were responsible for the popularization of the necrophagous properties widely associated with hyenas, being pictured as cemetery raiders. In today's popular western culture, particularly catalyzed by Disney's The Lion King and later Life of Pi, hyenas continue to be vilified through misrepresentations of their biology and ecology (Hugosson 2021).

In Africa, where humans and hyenas still coexist today, there is a generalized antipathy toward hyenas, with some exceptions (Baynes-Rock 2015b, 2016). Contrary to the scant appearance in pre-historic art, hyenas are common protagonists in African oral traditions where hyena maintains a transcultural meaning across multiple African Indigenous groups, with anthropomorphic roles that are ambivalent yet rather uniform across cultures (Tshabalala 2017). In these, hyenas are repeatedly portrayed as filthy, sly, greedy and necrophagous, embodying excessivity, ugliness and stupidity, sometimes foolish and humorous (e.g. Sapir 1981, Lawal 1996, Tshabalala 2017, Daasanach community 2019). They are the villains and foes of the stories. But they are also important metaphorical representations of dark or negative human behavior (Baynes-Rock 2016, Wako 2021). In this respect, many African stories still told traditionally today, play the dual role of teaching both values of human conduct and aspects of interspecific interactions, in this way transferring intergenerational collective knowledge and worldviews needed in these landscapes of coexistence (Fernández-Llamazares & Cabeza 2018). Remarkably, and coming back to our shared coexistence with wolves, tens of African hyena folktales have parallels in the Western stories where the wolf is the main villain (Ghosh 2014). And in the same way as wolves are associated with witchcraft in Western cultures (Davidson & Canino 1990), so are hyenas in many African and Asian cultures (Frembgen 1998), either through using hyena body parts in sorcery practices or by perceiving hyenas as witches and shapeshifters. Hyena tails are broadly used by sorcerers and thieves, while in many cultural contexts, witches are believed to ride hyenas at night. Examples are found amongst the Gusii of Kenya, the Zulu and Xhosa of South Africa, the Mbugwe, the Valangi or the Sukuma of Tanzania, and the Baluch in India, involving both spotted and striped hyenas (Frembgen 1998, Dunham 2006). It is no surprise, then, that this modern antipathy towards hyenas has "germinated and grown out of the detritus of human/hyena evolutionary history" (Baynes-Rock 2015b) and has persisted in stories, beliefs, and rituals so much so that they still confuse the two species where only one of the two is left (Száler 2024).

Perhaps it is no surprise that hyenas are hated, persecuted, and exterminated widely through various means, such as trapping, poisoning, gassing, or shooting. This aversion has been exacerbated by the increase in human-wildlife conflicts involving hyenas during the last decades, particularly with spotted hyenas. Following human population growth, land encroachment, and the declines of biodiversity, hyenas are more dependent than ever on humans, resorting to livestock depredation, or waste dumps (Sonawane *et al.* 2021, Torrents-Ticó *et al.* 2021, Torrents-Ticó 2023, Raycraft 2024). While the latter is seen as less of a problem, the former has aggravated negative attitudes also for the scavenging species. Striped hyenas and brown hyenas are reportedly targeted as subjects in human-wildlife conflicts (Alam *et al.* 2015, Weise *et al.* 2015, Bhandari & Bhusal 2017, Ashish *et al.* 2022), although claims of livestock depredation by these species are disputed and often stem from prejudices and misjudgments (Moures-Nouri *et al.* 2023). Similar misconceptions about aardwolves have also contributed to negative interactions (Yarnell & MacTavish 2013). Nevertheless, recalling that at least two of the hyenid species are near threatened, it has become clear that until hyenas are viewed in more positive light, it will be almost impossible to protect them (AbiSaid & Dloniak 2015, Wiesel 2015, Hugosson 2022, Wilkinson *et al.* 2024).

It is important to recognize, however, that interactions between people and hyenas are rarely simplistic and are not only shaped by negative interactions. Multiple ecosystem services provided by hyenas are increasingly recognized (Gade 2006, Moleón *et al.* 2014, Abraham *et al.* 2022, Sonawane *et al.* 2021, Panda *et al.* 2023) and hyenas still hold significant positive cultural importance in some societies (Frembgen 1998, Baynes-Rock 2015b). Perhaps we should turn towards the Horn of Africa once more, as one of the places where hyenas and humans have interacted the longest, and where they have developed intricate relationships that allow convivial coexistence (Baynes-Rock 2016).

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