

January 2014

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Research Article

Palaeopopulations of Late Pleistocene Top Predators in Europe: Ice Age Spotted Hyenas and Steppe Lions in Battle and Competition about Prey

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Received 21 March 2013; Accepted 11 June 2013

Academic Editor: Vlad Codrea

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Late Pleistocene spotted hyena *Crocota crocota spelaea* (Goldfuss, 1823) and steppe lion *Panthera leo spelaea* (Goldfuss, 1810) were top predators in Central Europe. The fossil record (2.303 hyena/1.373 lion bones = ratio 3/1) from 106 cave and open air sites demonstrates comparable associations to modern African hyenas/lions resulting in competition about prey and territory. Cannibalism within extinct spotted hyenas is well documented, including two individual skeletons. Those hyenas produced bone accumulations at dens. Feeding specializations on different megamammal groups are demonstrated for Late Pleistocene hyenas whose prey partly overlaps (e.g., cave bears) with those of lions and wolves. At most fossil sites, 1–3% of the lion remains indicate scavenging of lions by hyenas. The larger Late Pleistocene felids focussed on cervids (reindeers specialization during the high glacial = LGM), on bovids (steppe bison/aurochs), and possibly on saiga antelope and on the cave bear, hunting deep in caves during their hibernations and targeting cubs. The cave bear feeding was the target of all three top predators (lions, hyenas, and wolves) in the Late Pleistocene boreal forests which caused deathly conflicts in caves between them, especially with lions/hyenas and herbivorous cave bears that have no modern analogue.

1. Introduction

Pleistocene top predator research started in Europe with the first discoveries of “foreign animal finds” in the Zoolithen Cave (Germany) in 1774 when the German Priest Esper discovered some hyena (Figures 1–3), lion (Figures 4–6), wolf, and cave bear remains and explained them resulting from the “great deluge” [1]. Rosenmüller collected a large amount of cave bear remains including the *Ursus spelaeus* holotype skull [2] and the largest amount of lion material in the same cave [3]. This collection survived until today [2]. The French zoologist Cuvier interpreted in 1805 [4] some skull fragments from the German Zoolithen Cave as “hyena”. It was the German Paleontologist Goldfuss who described and named the first top predator of the Pleistocene with the holotype skull of the “cave lion *Felis spelaea*” in 1810 [5, 6]. In 1823 he published on the second large predator with the holotype skull of the “cave hyena *Hyaena spelaea*” [7]. Both of these skulls from the Zoolithen Cave were described in

more detail after their rediscovery in 2009 [8]. Finally, also the “cave wolf *Canis spelaeus*” was described in 1823 based on a cub skull found also in the Zoolithen Cave [7].

The modern era of “cave hyena” den research started in 1823, when the English Geologist Buckland published his “Reliquiae Diluvianae” [9]. Modern hyena den interpretation from historic times was based on mainly the famous Kent’s Caverns (E) and the König-Ludwigs Cave (D, there mentioned as “Kuhstall or Rabenstein Cave”) [9]. The German Biologist Giebel excavated hyena [10] and other faunal remains from Perick Caves (= Sundwig Cave, Sauerland Karst) in 1849–1852 in Germany and hyena and prey fauna remains from the Sewecken-Berge and Westeregeln (D) [11] open air gypsum karst areas of northern-central Germany. In 1863, Dawkins discovered the hyena bone-rich (467 remains, mainly teeth) and Neanderthal artefact bearing (e.g., bifaces) Wookey Hole Cave hyena den and overlapping Pleistocene Neanderthal human camp site (E) [12, 13]. Den research continued with the descriptions of the faunas of famous hyena

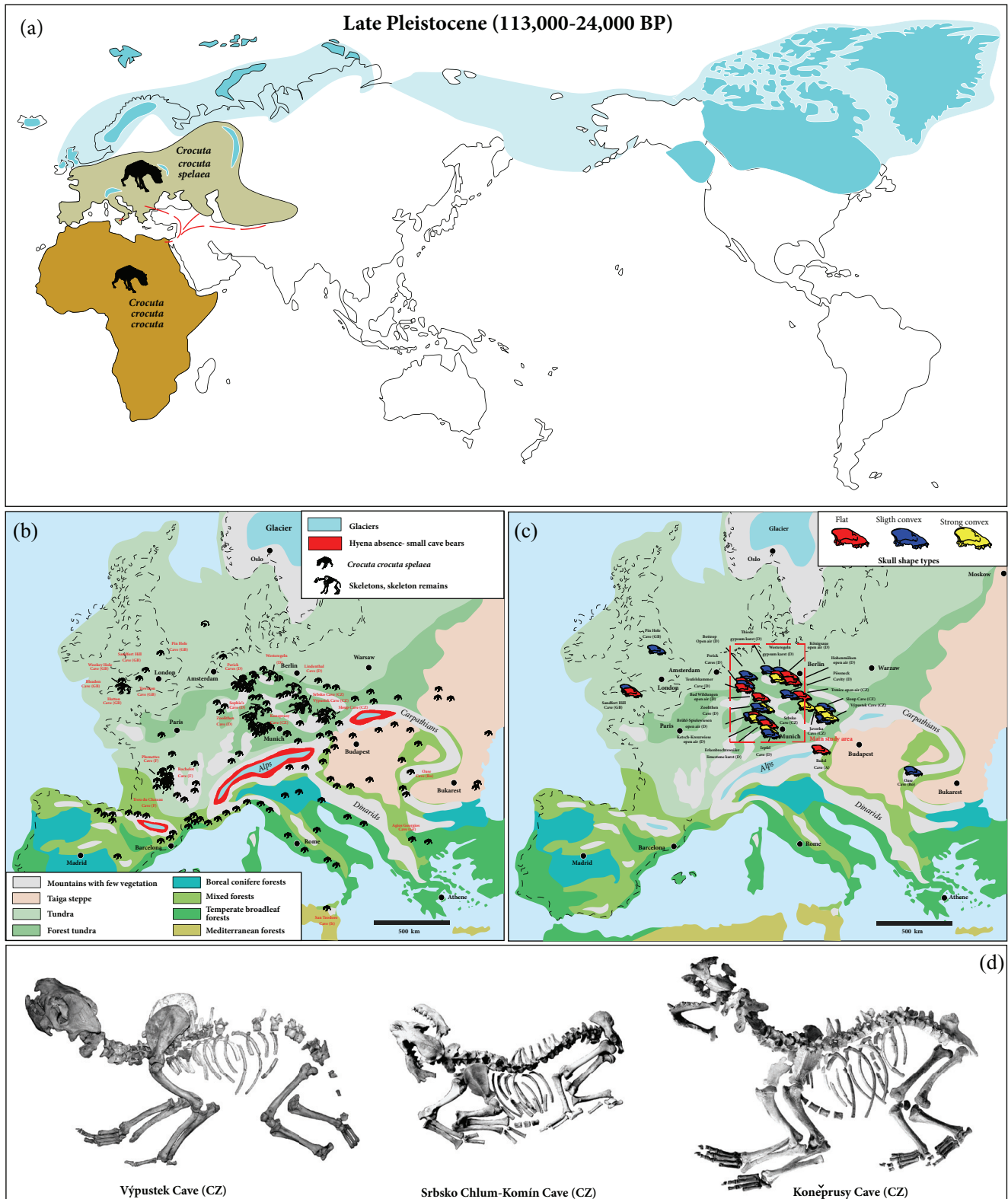


FIGURE 1: (a) Spotted hyenas globally during the Late Pleistocene. ((b) and (c)) Ice Age spotted hyena *Crocutea crocuta spelaea* (Goldfuss, 1823) sites in Europe during the Late Pleistocene before the Last Glacial Maximum (113,000–24,000 BP) with absence in alpine regions (= red areas). (d) Skeletons from Europe: adult individual skeleton from Vypustek Cave (Moravian Karst, CZ, coll. NHMW); composed cub skeleton from Srbsko Chlum-Komín Cave (Bohemian Karst, coll. NHMP); adult individual skeleton from Koněprusy Cave (Bohemian Karst, CZ, coll. NHMP).

den cave sites such as the Lindental Cave Gera (D) in 1867, where phosphatic excrement layers were reported and where fractured rhinoceros bones resulting from hyenas have been misidentified as “Pleistocene Neanderthal tools” [14]. This small cave also had artefacts from Neanderthals, which lead to historical conclusions that these nontool bones must be the “kitchen rubbish” of Pleistocene humans who “chewed on the bones” leaving bite marks (= “Osteodontokeratic culture” [15]). Nehring continued the German Late Pleistocene hyena research and collected some skulls and several postcranial hyena remains and prey bones from a new open air gypsum karst den site Thiede (D) [16] and at the Rösenbeck Cave (D) [17]. In 1892 Haarlé started the “hyena den” research in SE-France [18]. Reynolds published in 1902 [19] by far the best monograph on the English Late Pleistocene hyena remains of its time, but he confused some material as “individual skeletons” which are actually from at least two different caves, Wookey Hole [19, 20] and Sandfort Hill [19, 20] Caves (E). Two rediscovered skulls [17] from these two localities and a large collection which was hidden during the second World War under coals in the Somerset Museum [20] have not been analysed yet at present. The Teufelslucken Cave (A) was another hyena cave den and the first described from Austria in 1937 [21]. Zapfe presented in 1939 a paper on damaged bones by hyenas from different cave and open air sites, especially from Austria [22]. After the Second World War, new Late Pleistocene hyena dens were discovered in 1957 with the Torbryan Cave and Tonewton Cave (E) [20, 23]. In 1961, Thenius presented hyena damaged and chewed bones from Austria and critically discussed the “Osteodontokeratic culture” of the Tertiary Australopithecines (Hominidae), which were thought incorrectly to have produced hominid bite damage on bones, which were indeed made by hyenas [15]. The Czech Moravian Paleontologist Musil presented a further important monograph about the hyenas and their prey from the Sveduv Stül Cave hyena den (Moravian Karst, CZ) in 1962 [24]. In 1968 some articulated hyena prey remains from open air loess sites (= mammoth steppe) were mentioned from the site of Achenheim (D) [25], which convincingly demonstrated hyena activities outside the caves for the first time. Another southern German hyena den cave, the Aufhauser Cave, was 1982 shortly presented but remained not analysed [26]. In 1983, the first hyena remains were recovered with other Late Pleistocene bones on the seafloor of the North Sea by fishing boats [27]. In 1989, the Late Pleistocene hyena den Camiac Cave (F) was presented [28] and in 1992 another important hyena den from Agios Georgios Cave (Gr) [29]. The latter cave contained many Late Pleistocene horse and donkey remains that were the main prey of hyenas in a cub raising den site, but this was not well analysed in “hyena den context.” In 1996 in SW-France, especially Tournepiche began studies on “bone assemblages” to separate their human from carnivore genesis (or overlap) mainly at cave sites. He identified 16 Late Pleistocene hyena cave dens but did not follow qualitative prey or population structure analyses [30–33]. These include the cold period hyena prey fauna from Trou du Cluzeau Cave [30], Plumettes Cave [30], and the Eemian warm period prey fauna from Rochelot Cave [34]. In the latter hyena den, even Neanderthal human remains

(teeth and crushed longbone fragments) were found within the bovid/equid/suid dominated prey bone accumulation [34]. The most eastern known Late Pleistocene hyena den was reported in 2000 from the Prolom II Cave [35] in the Crimea, where there are hyena dens overlapping with human camp sites at cave entrances/portals. The overlapping often does not enable clear attribution to hyena prey or human kitchen rubbish. Interestingly, other hyena dens with possibly overlapping wolf dens were published for some Late Pleistocene Italian caves in 2004 [36]. Most probably instead the wolves were also prey and imported by hyenas, which is unsolved yet. The San Teodoro Cave on Sicily (I) was then presented in 2011, demonstrating the low marine sea level during the glacial of the Late Pleistocene which allowed the migration of hyenas to the island of present day [37]. Currant compiled several forgotten and new hyena dens from England in 2004, including the rediscovered Reynolds collections from World War II describing further caves as hyena dens such as Bleadon, Cavern, or Hutton Cavern [20]. A skull from Pin Hole [17] was added for English sites. In 2008 Polish hyena remains were compiled [38]. In the Czech Republic in 2004, the author’s “European Late Pleistocene spotted hyena project” provided an overview of Late Pleistocene hyena den types, mainly caves, which was presented for the Bohemian Karst mountainous region (= between 150 and 650 a.s.l.) near Prague [39]. In addition the most famous Czech Late Pleistocene caves and hyena remains, and first individual hyena skeletons, were reported from the Koněprusy Cave [40] and Srbsko Chlum-Komín Cave [41]. Recent hyena populations and prey analyses based on modern African spotted hyena ethology were used for the famous Sloup Cave [42] and the Výpustek Cave [42] in the Moravian Karst (CZ). In Germany, several important forgotten or overlooked hyena den cave (10 sites) and open air sites (2 sites) have been described in the past decade. These include the Sauerland Karst cave-rich region in northwestern Germany and 750 bones and 13 skulls mainly from the Perick Caves [10], Teufelskammer Cave [43], Balve Cave [44], and Rösenbeck Cave [17]. The most important Zoolithen Cave in the German Franconian Karst was also reviewed for its hyena [45] and hyena prey and lion [46] content, whereas the Franconian Sophie’s Cave [47] in that region supported the complex taphonomy solving between top predators and their scavenging and hunt of cave bears in Europe. To understand the life of extinct Late Pleistocene spotted hyenas outside the caves in lowlands of the Upper Rhine Valley [48], isolated remains were presented from river terrace gravel pit sites similar to the Münsterland Bay lowlands [49], whereas a population and its prey from the river terrace site Bottrop [50] is a key site with more than 3.000 bones to understand open air bone accumulations or dens and life of Late Pleistocene spotted hyenas, especially along rivers (river terrace den types). There, bones from gravel pit sites have been simply incorrectly attributed to “fluvial transport,” but perfect preserved bite damage and high amounts of chewed large mammal bones, such as those found in Bottrop or Selm-Ternsche and Herne along the Lippe and Emscher Rivers, demonstrate that these bone accumulations are similar as those in modern African from spotted hyenas along water

bodies. Other German open air hyena den and bone accumulation sites along ancient rivers and in loess mammoth steppe palaeoenvironments have been published. These include Bad Wildungen (there hyena birth den = recycled badger/fox dens in loess) [51] and Königsau (overlapping Neanderthal camp site) [52], whereas more recent studies have analyzed open air gypsum karst (Westeregeln [53], Sewecken-Berge [54]) and limestone karst dens (Fuchsluken Cavity [55], Wüste Scheuer Cavity [56]) to cover all morphological den types, especially those outside caves. Hyena scavenging sites with remains of their largest prey (woolly rhinoceros carcass-Krölpa [56], woolly mammoth carcass-Siegsdorf [57], and forest elephant carcasses-Neumark-Nord Lake 1 [58]) demonstrate the top predator butchering technique and deathly conflict with lions over prey.

Late Pleistocene lions were described for the first time in 1810 based on a skull (Figure 5) from the Zoolithen Cave hyena and cave bear den (D) [5]. Because these initial finds were from caves, they were historically named “cave lions,” which was revised recently to “steppe lion” [8]. In 1900, the most northern single tooth and bone remains of lions from English hyena den caves were presented in a monograph [69]. In 1906, “cave lion” remains from France were published [70]. A single skull was then reported from the Genther Cave, a cave bear den in Upper Franconia (D) in 1953 [71]. In 1968, a discussion between the comparison of lion remains from the German/European “Pleistocene” and modern African lions resulted in the determination that the “Pleistocene” forms (it was generalized) must have been slightly larger (1/4) than modern ones [72], which is the truth only for the Middle Pleistocene (Saalian glacial) *P. leo fossilis* subspecies, indeed. In 1957, Late Pleistocene lions were then attributed to the modern lion subspecies, as *P. leo spelaea*, osteometrically based on new material from France [73]. In 1983, fishing boats recovered many Pleistocene mammal bones, including lion remains, on the seafloor of the North Sea [27]. The first Late Pleistocene individual lion skeleton was then discovered in Arrikutz (Es) in 1981 [74], with an additional skeleton in Austria [75]. Lion skulls and postcranial remains were published by Argant in 1988 from the cave bear den Aze Cave (F), which contained Middle/Late Pleistocene material mixed, including some Middle Pleistocene *P. leo fossilis* remains [76]. Another skeleton from a large male lion was found before 1992 beside a mammoth carcass at the open air site of Siegsdorf (D) [77]. Cranial and postcranial bones followed from a cave excavation in the German cave bear den site of Hermann’s Cave [78]. From Croatia, lions were compiled with single remains from several cave sites without clear taphonomic context [79]. Further to the east in Yakutia, the first “cave lions” (not even “steppe lions,” instead another subspecies *P. leo vereshchagini*) were reported from open air localities [80]. Another single *P. l. spelaea* lion skull was recovered in Zandobbio (It) dating to the Eemian interglacial [81]. From Czech Republic, remains were compiled in 2007 from several open air (e.g., Praha) and hyena den cave sites [63]. In 2008, an overview of Polish lion remains was presented, again without a clear understanding of their taphonomy [38]. The first European “skeletons” were published from the Sloup Cave hyena and cave bear den (CZ), which new studies

revealed both composite skeletons of different individuals [62]. The only individual skeleton is from the Srbsko Chlum-Komin Cave, representing an early adult lioness (Figure 4) with evidence of a brain case trauma injured animal [62]. This skeleton is important for understanding the conflict between both top predators, especially at cave den sites. Several skulls and postcranial remains were analyzed for sexual dimorphism and taphonomic context, especially from cave bear and hyena den sites in Germany, where for the first time the hyena-lion antagonism and scavenging of lion carcasses by hyenas were discussed [64, 82, 83]. The most important new discoveries in 2009 were three lion skeletons in different taphonomic situations found deeply within the entrance of a cave bear hibernation plateaus in the Romanian Urşilor Cave [84]. This discovery yielded a clear evidence for the active hunting of hibernating cave bears by lions deep in larger and complex cave systems [65]. Further important is the open air site discovery of a diseased older lioness (Figure 4) in between the Eemian interglacial elephant graveyard Neumark-Nord Lake 1. This skeleton was interpreted to have resulted from a hyena/lion conflict over their largest prey [61]. The incorporation of lion remains at overlapping hyena den and human camp sites was discussed critically for the Balve Cave (D) [85], where it was incorrectly believed that Neanderthals/Aurignacian modern Pleistocene Late Palaeolithic humans imported “lion furs” after their kills to the camp site. Indeed, those lion remains were later demonstrated to have resulted from hyena and cave bear conflicts. A listing and analysis of some material without clear taphonomy, including a single skull (Bešeňová Cave), were compiled from ten Slovakian caves [86]. The largest European Late Pleistocene lion fossil record (= palaeopopulation) was recently described in 2011 for Zoolithen Cave, where evidence for cave bear hunting by lions was established by taphonomic studies [44]. Open air lion material was then reviewed for northern Germany for all kind of sites (Figure 4), of which several bones had also bite damages indicating scavenging and even importation of lion body parts to their dens by Late Pleistocene spotted hyenas [67]. In northern Germany, the only known Late Pleistocene lion trackway has been documented with other Late Pleistocene megafauna tracks at Bottrop, where additionally partly chewed and damaged lion remains have been described [67]. From the Upper Rhine Valley (D) three more skeleton remains and several bones have been reported in 2012 [66]. Here, a new unpublished skull is added of a lioness from the Austrian Badel Cave, another hyena and cave bear den, but also a skull from the Austrian Mixnitz Cave, or Upper Rhine Graen open air sites, such as finally the smallest and most rare cranial material of sibling and cub remains from Swabian caves of southwestern Germany (Figure 5).

Additionally, in the Late Pleistocene, there were large wolf “ecomorphs” [87] which glacial subspecies *Canis lupus spelaeus* Goldfuss, 1823) [6] was not yet revised, as third largest carnivores. Their ecology is still only beginning to be understood, especially for their cave occupation: den use for cub raising or import as prey by hyenas especially in boreal forest environments [36, 47, 87]. At the Sophie’s Cave (D), clear evidence for cave bear scavenging activity was presented

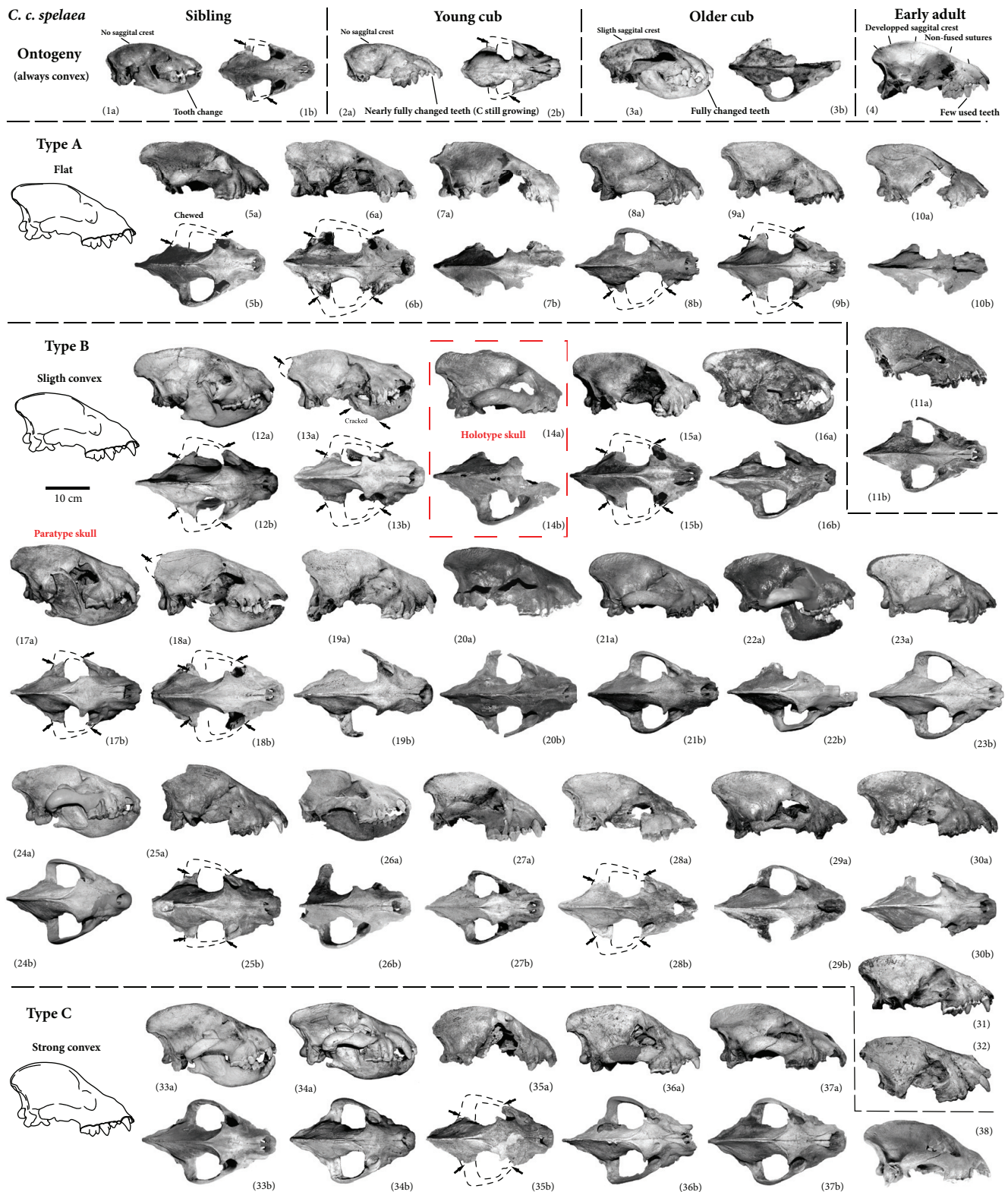


FIGURE 2: *Crocuta crocuta spelaea* (Goldfuss, 1823) ontogenetically skull shape change and three main skull shape types across Europe (composed from [17] and new material). (1) Sibling skull (with cannibalistic damage) in tooth change from Srbsko Chlum-Komín Cave, Czech Republic (NMP No. R3779), (a) lateral and (b) dorsal. (2) Young cub with last tooth change of the canine from Ukraine (UZM without no.), (a) lateral and (b) dorsal. (3) Skull of an older cub with fully changed permanent dentition from Perick Caves, Germany (SNSD No. Sundwig-15), (a) lateral and (b) dorsal. (4) Skull of an early adult with few used teeth and still unfused brain case sutures from Badel Cave, Austria (MOM No. F1), dorsal. (5) Skull (with cannibalistic damage) of a male from Perick Caves, Germany (BMNH No. 28557), (a) lateral and (b) dorsal. (6) Skull (with cannibalistic damage) from Perick Caves, Germany (SNSD Sundwig-14), (a) lateral and (b) dorsal. (7) Skull from Teufelskammer Cave, Germany (RE No. 554 791 A1005), (a) lateral and (b) dorsal. (8) Skull (with cannibalistic damage)

from Erkenbrechtsweiler open air karst site, Germany (SMNS No. 19062a), (a) lateral mirrored and (b) dorsal. (9) Early adult female skull (with cannibalistic damage) from Bad Wildungen-Biedensteg open air site, Germany (HMBW No. Bi-52/45), (a) lateral mirrored and (b) dorsal. (10) Skull of a male from Trmice open air loess site, Czech Republic (MB.Ma.902), (a) lateral and (b) dorsal. (11) Adult skull from Königsau, Germany (LSDA No. HK-62 : 248), (a) lateral and (b) dorsal. (12) Old adult female skull (with cannibalistic damage) from Döbritz Cave, Germany (MB No. Ma.44381), (a) lateral and (b) dorsal. (13) Old adult skull (with cannibalistic damage) of a female from Perick Caves, Germany (NMB No. Heinr-1), (a) lateral and (b) dorsal. (14) Adult skull from Zoolithen Cave, Germany (GMB No. M.2609; Holotype in Goldfuss, 1823), (a) lateral and (b) dorsal. (15) High adult skull (with cannibalistic damage) of a female from Perick Caves, Germany (BMNHL No. 28558), (a) lateral and (b) dorsal. (16) Adult skull, with lower jaw, of a female from Sloup Cave, Czech Republic (NHMW No. 2008z0087/0000), (a) lateral mirrored and (b) dorsal. (17) Old adult skull of a female with lower jaw (with cannibalistic damage) from Zoolithen Cave, Germany (UE No. GL 77/203 and 28/509; Paratype in Diedrich, 2011e). (18) Old adult skull (with cannibalistic damage) from Sandfort Hill Cave, England (TM No. 44/1995/695; original to Reynolds, 1902), (a) lateral and (b) dorsal. (19) Old adult skull (with cannibalistic damage) from Sandfort Hill Cave, England (TM No. 45/1995/407; original to Reynolds, 1902), (a) lateral and (b) dorsal. (20) High adult skull from Thiede open air gypsum karst site, Germany (MB No. Ma.49139.1), (a) lateral mirrored and (b) dorsal. (21) High adult skull of a male from Ketsch-Kreuzwiese Rhine River terrace open air site, Germany (SMNS No. 6617.73.62.1), (a) lateral and (b) dorsal. (22) Old adult skull-composite from Bottrop open air site and Emscher River terrace open air site, Germany (MFUOB without No.), (a) lateral and (b) dorsal. (23) High adult skull of a female from Oase Cave, Romania (SIRB No. Oases crocuta-1), (a) lateral and (b) dorsal. (24) High adult skull from Irpfel Cave, Germany (SMNS No. AH262), (a) lateral mirrored and (b) dorsal. (25) Adult skull (with cannibalistic damage) from Sloup Cave, Czech Republic (NHMW No. 2008z0087/0002), (a) lateral mirrored and (b) dorsal. (26) High adult skull of a male from Westeregeln gypsum karst open air site (MLU.IFG No. WEgeln-13A-B), (a) lateral and (b) dorsal. (27) Adult skull from Badel Cave, Austria (WMM No. F2), (a) lateral and (b) dorsal. (28) Deformed high adult skull (with cannibalistic damage) of a female from Bad Wildungen-Biedensteg open air site, Germany (HMBW No. Bi-10at), (a) lateral and (b) dorsal. (29) High adult skull of a female from Gernsheim, Germany (MSG without no.), (a) lateral (mirrored) and (b) dorsal. (30) High adult skull from Doesburg near Arnheim, Germany (RE without no.), (a) lateral (mirrored) and (b) dorsal. (31) Young adult skull from Pin Hole Cave, England (MMU No.65/7), lateral mirrored. (32) Adult skull from the Mladeč Cave, Czech Republic (AMB No. 2644), lateral. (33) Young adult skull of a female from Srbsko Chlum-Komín Cave, Czech Republic (NMP No. R1067), (a) lateral and (b) dorsal. (34) Old adult skull from the female skeleton of Výpustek Cave, Czech Republic (NHMW No. A5529), (a) lateral mirrored and (b) dorsal. (35) Adult skull (with cannibalistic damage) from the Javorka Cave, Czech Republic (AMB No. OK114891), (a) lateral and (b) dorsal. (36) High adult skull (with frontal bite impact in the process of healing) from Irpfel Cave, Germany (SMNS No. 7.801), (a) lateral and (b) dorsal. (37) High adult skull of a male from Gernsheim, Germany (MSG without no.), (a) lateral (mirrored) and (b) dorsal. (38) Senile skull with P^4 dental pathology from Crumstadt, Germany (HLMD without no.), lateral.

based on bone fragments found in excrements and within a faecal place where wolves even used a part of a cave bear den (several meters deep from the entrance area) over a short period obviously as den [47].

2. Materials and Methods

2.303 hyena and 1.373 lion bones of Late Pleistocene age from 106 studied cave and open air localities in Central Europe were analysed mainly from prey bone assemblages of several German and Czech hyena dens (Table 1). This study and review used an interdisciplinary approach apart from classical “bite mark analyses on single bones”, rather it used the newly developed “butchering decomposition and bone damage stage” analyses. New results started with the rediscovery of many historically collected bones of the Late Pleistocene predators and prey remains, which were reidentified for the first time as hyena den origin. Hyena populations were analysed, along with the bone assemblages. The study of all animal groups based on NISP (= number of identified specimens per taxon) and partial MNI (= minimum number of individuals) analyses were also the basis to distinguish den site types using the modern hyena/lion ethology comparison. Important for the results was the study of different topographic related hyena den morphotypes: caves open air, river terrace, loess, and gypsum karst sites. The historical collections are highly useful for these analyses, and in several cases two things were important for their modern analyses use: (1) bones from different collections were

compiled from different museums; this often demonstrated the anthropogenic selection of “good bones” and “bad bones” (bone fragments), but in hyena den analyses the complete assemblage is required for interpretations. In some cases the historical sites were completely restudied at the existing sites such as the Zoolithen Cave, Sophie’s Cave, Srbsko Chlum-Komín Cave, Sloup Cave, Westeregeln open air, and Sewecken-Berge open air, where additional excavations and stratigraphic/sedimentological and C14 dating work were important to understand the age, bone taphonomy, and site genesis in general. In total, several tens of thousands of bones were analysed since 2004 from three main study areas (Sauerland Karst, Thuringian Karst, Bohemian and fewer Moravian Karst, Franconian Karst, small area in the Carpathian Apuseni Mountain karst, and open air sites in Germany/Czech Republic). As part of those studies the holotype skulls of *C. c. spelaea*, *P. l. spelaea*, and *U. s. spelaeus* were rediscovered in the famous Rosenmüller 1794 collection. Other forgotten rediscovered German hyena den site collections are from Giebel 1844–1848 (Westeregeln, Sewecken-Berge), Nehring 1872 (Thiede, Westeregeln), or Müller 1902 (Fuchsluken Cavity). This large amount of material studied is no more at the former Preußische Geologische Landesanstalt Berlin (now coll. MB). Additionally, all the mostly overlooked individual skeletons of hyenas/lions have been identified, prepared, and composed by the author in the past years in various collections. The main important and relevant sites are listed (Table 1) at which material is housed in the following institutions of different countries: Austria:

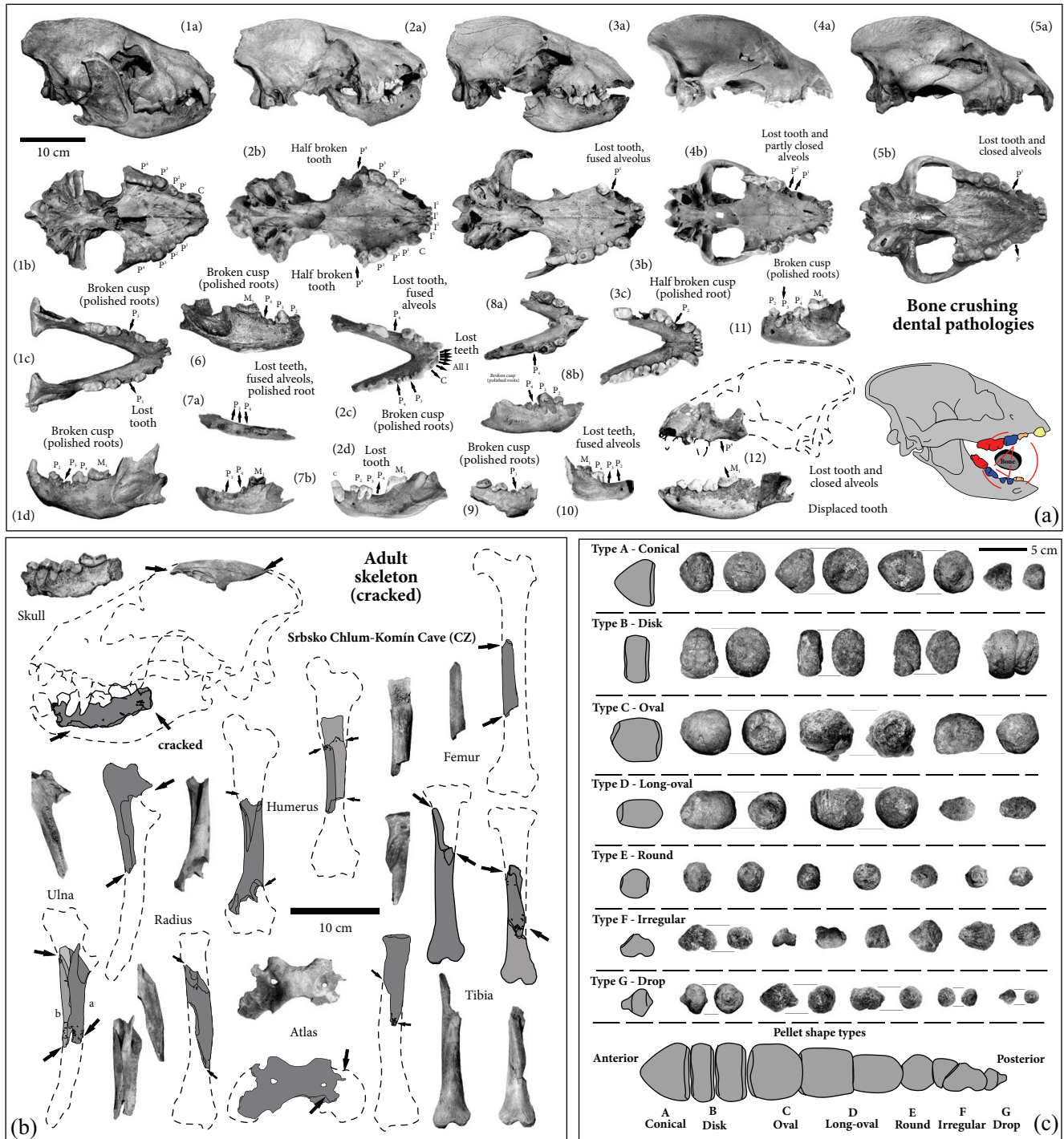


FIGURE 3: (a) *Crocota crocuta spelaea* (Goldfuss, 1823) dental pathologies on skulls and lower jaws. Main damages are found on the premolars (bone crushing) and the incisors/canines (nibbling) (composed after [59]). (1) Paratype skull of an adult with lower jaw from the Zoolithen Cave, Germany (UE No. GL 77/203 and 28/509), (a) lateral, (b) ventral, (c) lower jaw dorsal, and (d) lower jaw lateral. (2) Skull with lower jaw of a senile from Perick Caves, Germany (NMB No. Heinr-1), (a) lateral, (b) ventral, (c) lower jaw dorsal, and (d) lower jaw lateral. (3) Skull of an old adult from Sandfort Hill Cave, England (TM No. 44/1995/695; original to Reynolds, 1902), (a) lateral, (b) ventral, and (c) lower jaw dorsal. (4) Senile skull from Crumstadt, Germany (HLMD without no.), (a) lateral and (b) ventral. (5) High adult skull from Gernsheim, Germany (MSG without no.), (a) lateral (mirrored) and (b) ventral. (6) High adult right mandible from the Perick Caves, Germany (GMB no. M2565), lateral. (7) Senile left mandible from the Wilhelms Cave, Germany (GMB no. M5999 (Mandible)/GPIM no. A5F1281 (M1), (a) lateral and (b) dorsal. (8) High adult mandible from the Sewecken-berge open air gypsum karst, Germany (MB no. Ma 29606), (a) dorsal and (b) lateral. (9) High adult right mandible from the Grünmann's Cave, Germany (GMB without no.), lateral. (10) Senile right mandible from the Perick Caves, Germany (SNSD no. Sundwig-44), lateral. (11) High adult left mandible from the Wilhelms Cave, Germany (EMSCH No. Frettertal-1), lateral. (12) Adult maxillary and mandible from the Reporje Kalvarie Cave, Czech Republic (NMP no. 5473/R 12 and 111), lateral. (b) By Ice Age spotted hyenas cannibalistic scavenged and cracked hyena carcass from the Srbsko Chlum-Komín Cave hyena den, Czech Republic (modified after [41]). (c) Ice Age spotted hyena coprolite type shape types (modified after [60]).

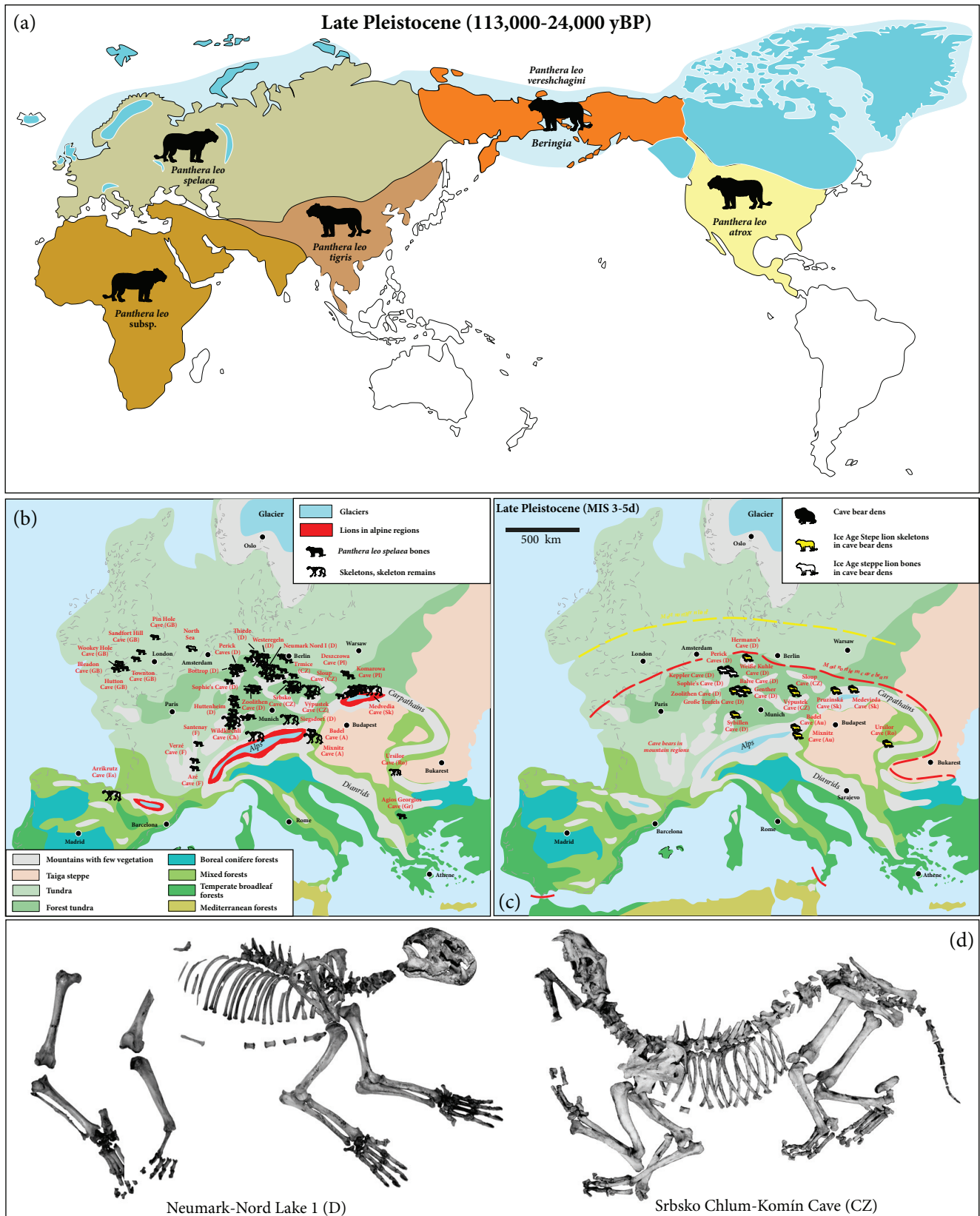


FIGURE 4: Ice Age steppe lion *Panthera leo spelaea* (Goldfuss, 1810) distribution (a) worldwide and (b) important sites in central Europe during Early/Middle Late Pleistocene before LGM (113.000–24.000 BP) (composed from different sources; see reference list). (c) Lion skeletons and remains in Late Pleistocene cave bear dens of Europe. (d) Articulated diseased lioness skeleton from Neumark-Nord Lake I (D) elephant graveyard (from [61]) and subadult diseased lioness from Srbsko Chlum-Komín Cave hyena den (CZ) (from [62]).

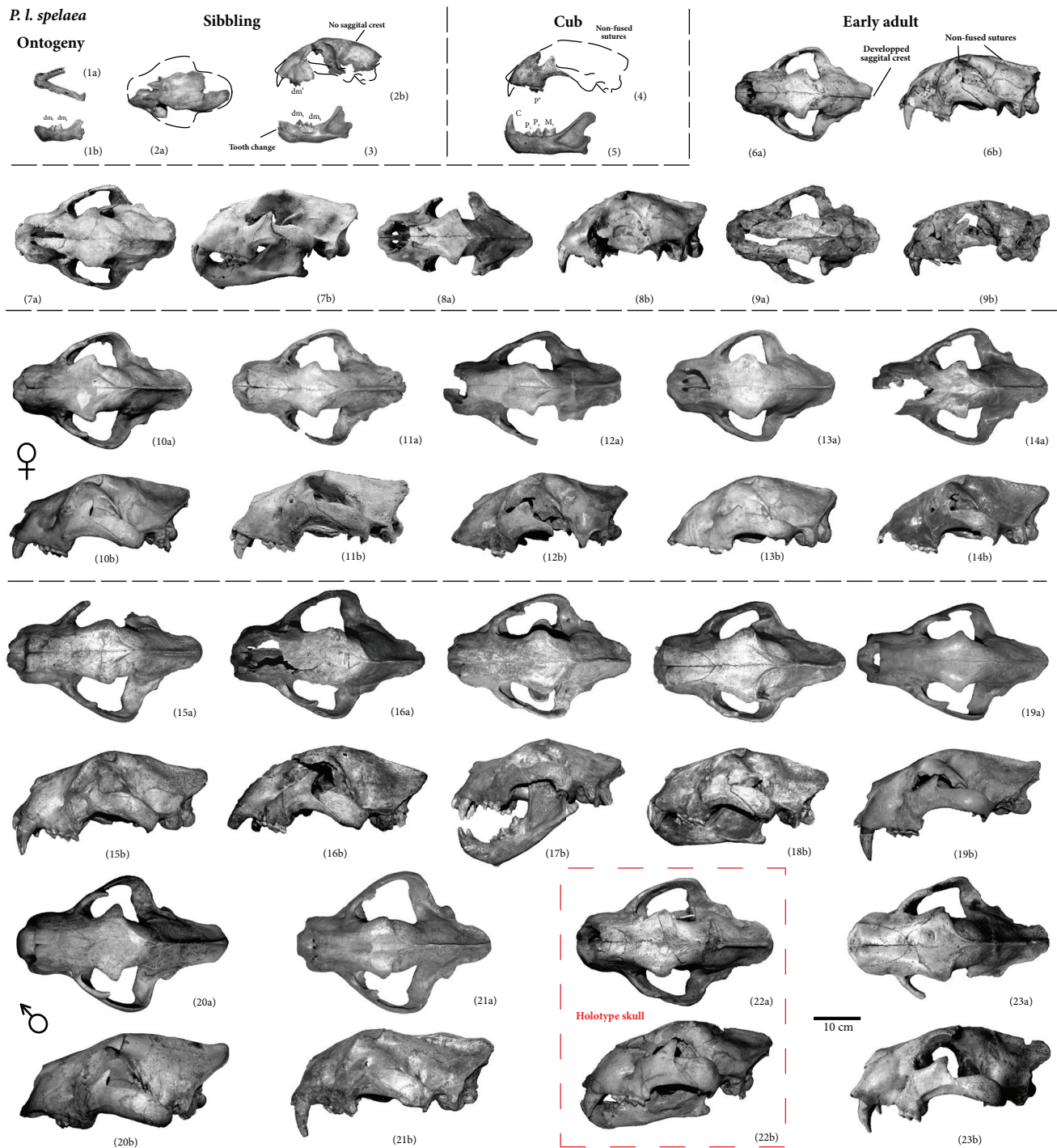


FIGURE 5: *Panthera leo spelaea* (Goldfuss, 1810) ontogenetically skull shape change and three main skull shape types across Europe (composed from [8, 46, 62–66] and herein added new material: 1–3, 10, 13, 16 and 20). (1) Sibling lower jaw from the Mixnitz Cave cave bear den, Austria (RE no. NMB 108a), (a) dorsal and (b) lateral. (2) Incomplete sibling skull from Aufhäuser Cave hyena den, Germany (SMNS without no.), (a) dorsal and (b) lateral. (3) Sibling mandible with milk dentition from Hohlenstein Cave hyena den, Germany (SMNS no. 33226), lateral. (4) Cub maxillary with permanent dentition from Zoolithen Cave hyena and cave bear den, Germany (UE no. Sp 42/14), lateral. (5) Cub mandible with permanent dentition from Zoolithen Cave hyena and cave bear den, Germany (UE no. GL 77/85), lateral. (6) Early adult skull from a skeleton of Urşilor Cave cave bear den, Romania (SIER no. PU/0001), (a) dorsal and (b) lateral. (7) Early adult skull with lower jaw from a skeleton of Srbsko Chlum-Komín Cave hyena den, Czech Republic (NMP no. R4406), (a) dorsal and (b) lateral. (8) Early adult skull from the Perick Caves hyena and cave bear den, Germany (BMNHL no. 28553), (a) dorsal and (b) lateral. (9) Early adult skull from Beroun-Hýskov open air river terrace site, Czech Republic (MBKB no. 363a), (a) dorsal and (b) lateral. (10) Adult skull from Zoolithen Cave hyena and cave bear den, Germany (MB no. Ma.50947), (a) dorsal and (b) lateral. (11) Adult skull from Badel Cave hyena and cave bear den, Austria (MOM no. F1), (a) dorsal and (b) lateral. (12) Adult skull from Sloup Cave hyena and cave bear den, Czech Republic (AMB no. OK130570), (a) dorsal and (b) lateral. (13) Senile skull from Campusal Cave, Romania (SIER without no.), (a) dorsal and (b) lateral. (14) Adult skull from

Bobenheim-Roxheim open air river terrace, Germany (RE no. PCC 132), (a) dorsal and (b) lateral. (15) Adult skull from Zoolithen Cave hyena and cave bear den, Germany (UM-O no. BT5421), (a) dorsal and (b) lateral. (16) Senile skull with several dental pathologies from Hermann's Cave cave bear den, Germany (NMB no. 1794-M), (a) dorsal and (b) lateral. (17) Adult skull (mounted in composite skeleton) from Sloup Cave hyena and cave bear den, Czech Republic (AMB without no.), (a) dorsal and (b) lateral. (18) Adult skull (mounted in composite skeleton) from Sloup Cave hyena and cave bear den, Czech Republic (NHMV no. 1885/0014/4302), (a) dorsal and (b) lateral. (19) Adult skull of a skeleton from Huttenheim open air river terrace site, Germany (SMNS no. 6816.5.6.73.1), (a) dorsal and (b) lateral. (20) Adult skull of a skeleton from Edingen (Brühl) open air river terrace site, Germany (SMNS no. 6617.1.9.72.2), (a) dorsal and (b) lateral. (21) Adult skull from Mixnitz Cave cave bear den, Austria (RE no. NMB 107), (a) dorsal and (b) lateral. (22) Holotype skull with bite mark damage pathology of an adult male from Zoolithen Cave, Germany (MB no. Ma.50948), (a) dorsal and (b) lateral. (23) Adult skull from Zoolithen Cave hyena and cave bear den, Germany (MB no. Ma.48155.1), (a) dorsal and (b) lateral.

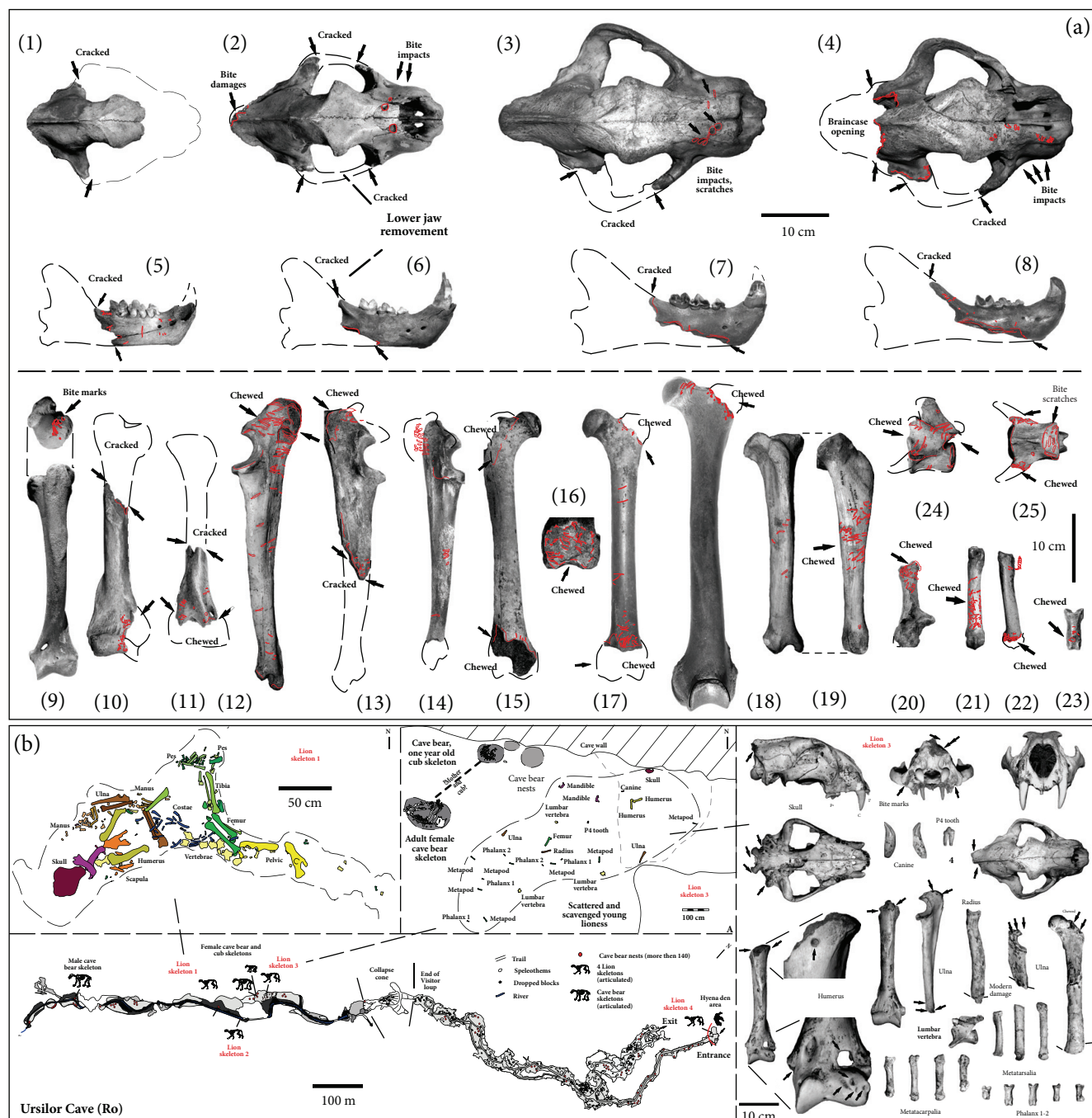


FIGURE 6: Ice Age steppe lion postmortem bite damages on (a) cranial and postcranial bones and (b) skeleton of a subadult (scavenged and scattered besides mother and cub on place skeletons on hibernation plateau) deep in the Urşilor Cave (Ro) (composed from [65, 67]).

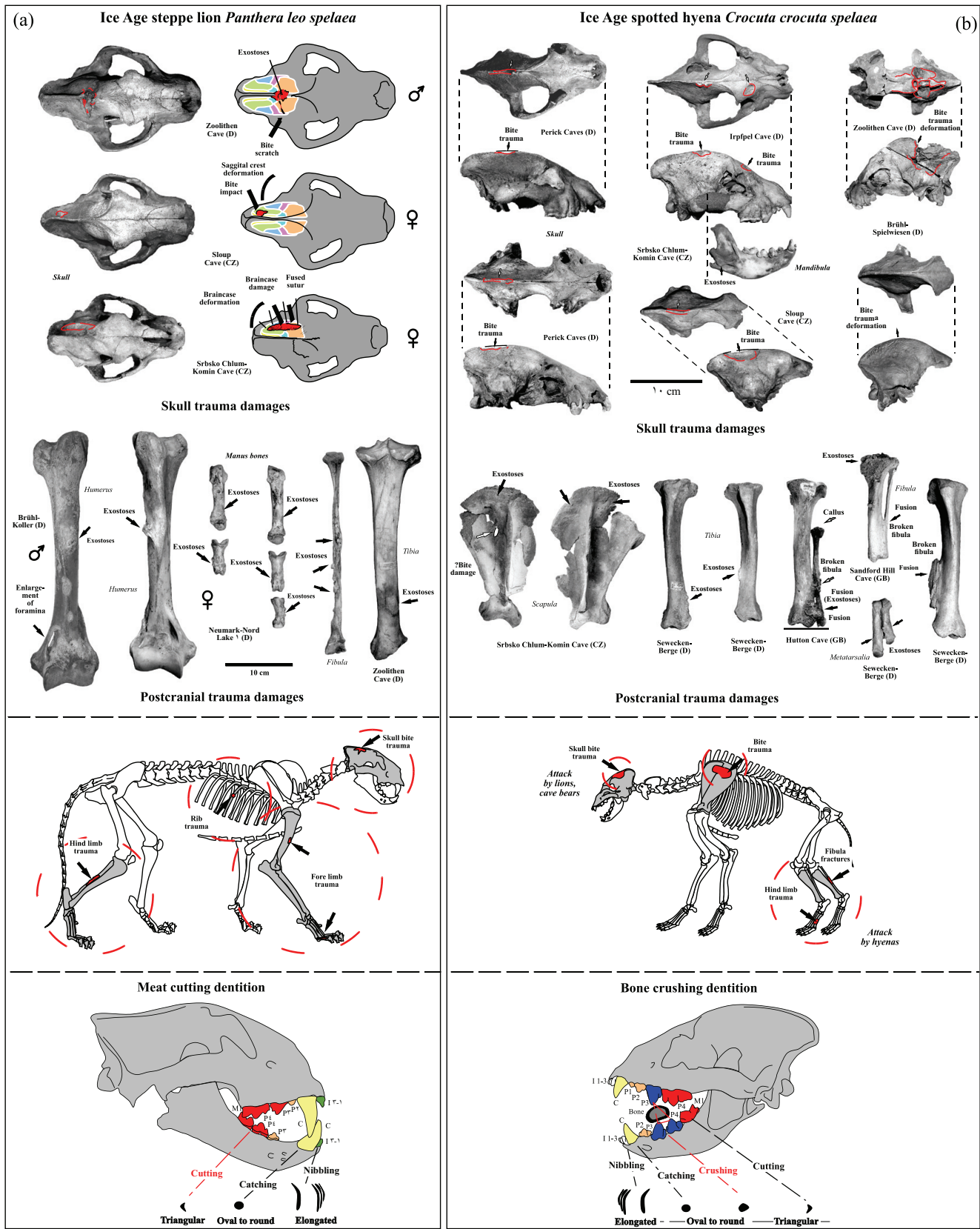
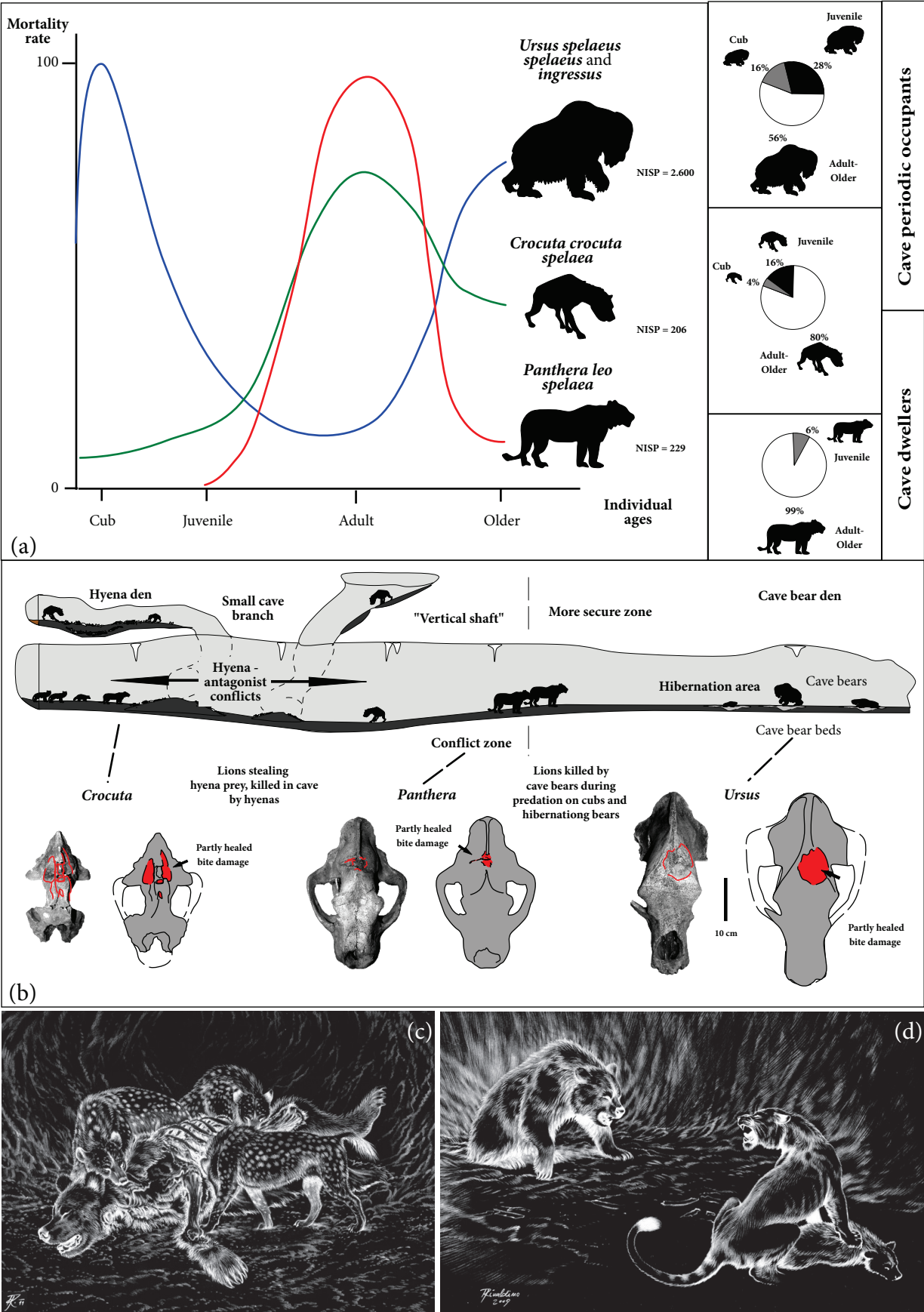


FIGURE 7: (a) Ice Age steppe lion and (b) Ice Age spotted hyena alive trauma pathologies (bite damages mainly) from different sites caused by hyenas, lions, and cave bears due to bite damages in battles in and outside of caves (compiled partly from [59, 68]).



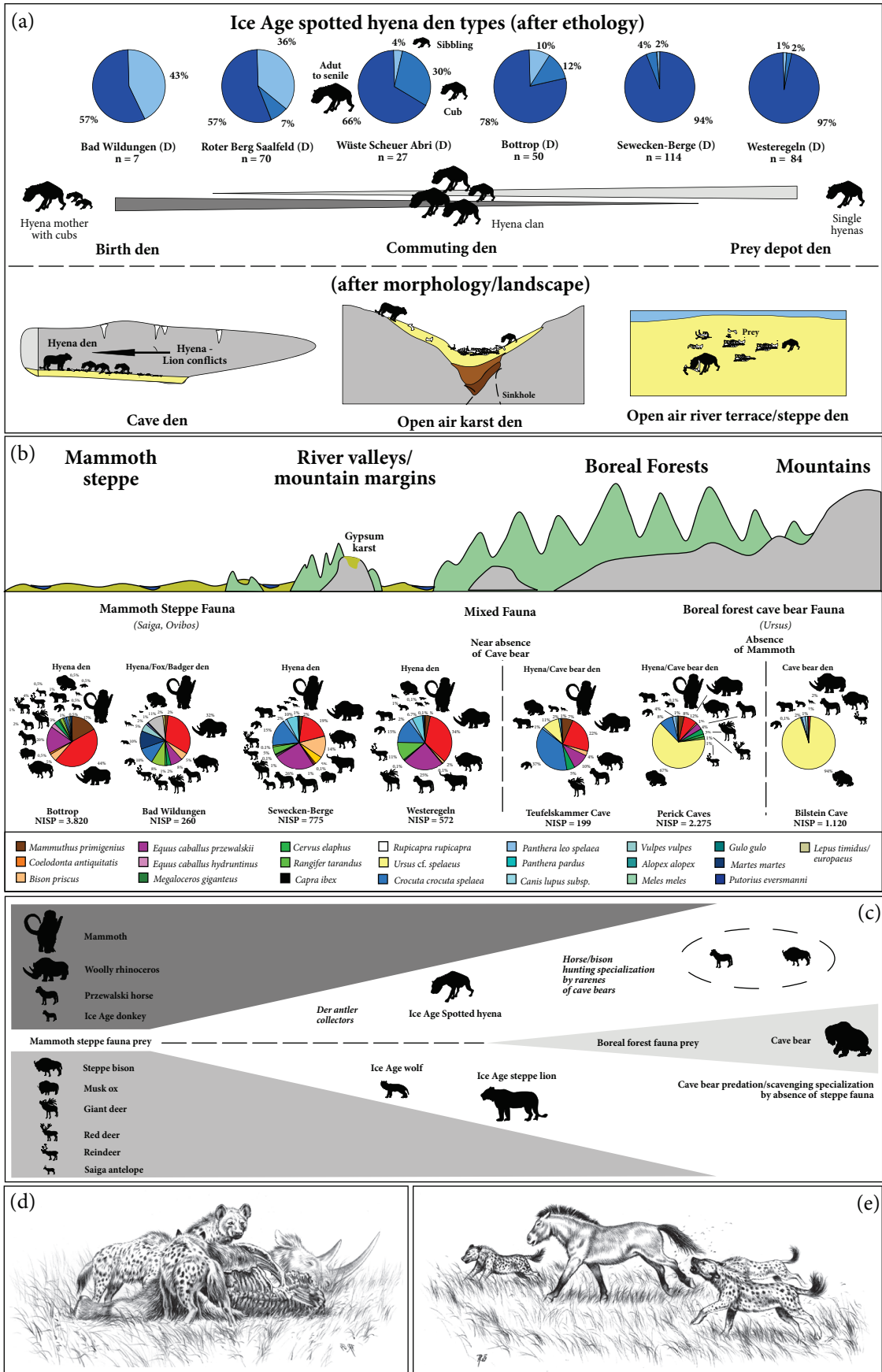


FIGURE 9: (a) Ice Age spotted hyena den types after ethology and landscape and morphology. (b) Hyena prey bone assemblages and (c) prey specialization in mammoth steppe lowland and boreal forest mountains. (d) Ice Age spotted hyenas decomposing in butcher technique a woolly rhinoceros carcass. (e) Ice Age spotted hyena clan hunting Przewalski horse (illustrations G. “Rinaldino” Teichmann).

NHMH = Natural History Museum Vienna; Czech Republic: AMB = Anthroposmuseum Brno, MBKB = Museum of the Bohemian Karst Beroun, and NMP = National Museum Prague; England: BMNH = British Museum of Natural History London, England, SM = Somerset Museum; Germany: BM = Balve Museum, GMB = Goldfussmuseum Bonn, GPIM = Geological-Paleontological Museum of the Westphalian Wilhelms University Münster, GZG = Geolocal Centrum Göttingen, HC = Heinrichs Cave Hemer, LDA = Landesmuseum für Archäologie Saxony-Anhalt, LM = Löbbecke Museum Aquazoo Düsseldorf, ME = private collection Menger, MLUIFG = Martin-Luther-University Institute for Geosciences Halle/Saale, MMS = Mammut-Museum Siegsdorf, MNB = Museum for Nature and Humans Bielefeld, MUOB = Museum Pre- and Local History Bottrop, MSG = Museum Schöffersstadt Gernsheim, RE = private collection Reiss, SNMB = Staatliche Naturhistorische Museum Brunswick, SMNS = Staatliche Museum Naturkunde Stuttgart, SNSD = Staatliche Naturhistorische Sammlungen Dresden, UE = University Erlangen, UZM = Urzeitmuseum Taufkirchen, U-MO = Oberfränkische Urweltmuseum Bayreuth, and ZO = Forschungsgruppe Höhle und Karst Franken e.V., Nürnberg; Romania: USC = Urşilor Cave, SIER = Speleological Institute Emil Racvita Bucharest; USA: MOM = Museum of Man.

3. Late Pleistocene Spotted Hyenas

The hyenas of the European Late Pleistocene were popularised historically as “cave hyenas” with the latin binomial name “*Hyaena spelaea*,” because of their initial discoveries in the Zoolithen Cave (D) [6] and other caves in Europe. Recent revision according to modern taxonomic [89] and DNA [90] studies has considered these Late Pleistocene spotted hyenas as *Crocota crocuta spelaea* (Goldfuss, 1823) [45]. These Late Pleistocene hyenas are slightly differed to modern spotted hyena subspecies, with those in the Eemian interglacial being smaller and the Weichselian glacial larger [91, 92]. Similar to modern spotted hyenas, the females in the extinct species [93] are larger [45, 94], which is also reflected in the skull record of Europe for the Late Pleistocene spotted hyenas (Figure 2) [17].

3.1. Hyena Populations over Europe. In the study area of Germany and Czech Republic, the Late Pleistocene fossil record includes 2,303 bones and 2 skeletons from hyenas (Table 1). These predators must have migrated from Africa to the North and were distributed all over Eurasia up to northern England (most northern den in Pit Hole Cavern (GB)) during the Late Pleistocene (Eemian interglacial to Weichselian/Wuermian glacial, 126.000–24.000 BP). The last hyenas of Europe must have become extinct just before the Last Glacial Maximum (= LGM, around 22,000 BP) [93] at least in northern Europe. A retreat to the south is not really expected, while an eastern migration is not yet supported by studies from Asia with most eastern records in the Altai Mountains. In most cases except in the well studied regions of Germany and Czech Republic, where hyena remains are

found, they occur at den sites even though they have been mostly overlooked (Figure 1). An overview of more than 120 Late Pleistocene hyena den sites (Figure 1) indicates much more small caves and entrances of larger caves to have been used, whereas the rare open air record is mostly a result of bone taphonomy accumulation misidentification. Not all sites are dated properly, but they likely represent the Late Pleistocene interval.

3.2. Holotype, Paratype Skulls, and Skeletons. The recently rediscovered holotype skull of “*Hyaena spelaea*” was found in the Zoolithen Cave of Bavaria (D) [6]. Besides this toothless, old individual, and historically damaged skull, a paratype skull was selected from a large hyena palaeopopulation of this cave [44]. From this cave, similar to many other sites of Europe, articulated skeletons are absent due to two reasons: (a) nonprofessional excavation and collecting and (b) hyena cannibalism. More recently, a fairly complete individual skeleton of an adult animal was rediscovered and composed from the Koněprusy Cave (CZ) [40] (Figure 1). Another skeleton with a better preserved skull was chosen from the Výpustek Cave (CZ) [41] (Figure 1). Skelton remains of three different cub/sibling individuals were used from the Srbsko-Chlum-Komín Cave [41], to build a first composite cub skeleton of this species (Figure 1), which is important for the identification of overlooked cub bones in various collections. Further incomplete hyena skeletons seem to have been present also in the Perick Caves, Hutton Cavern, and Zoolithen Cave, but cannibalism, river floods, or historical excavations destroyed their articulation context.

3.3. Skull Shape Types. Recent studies on both, modern African spotted hyenas [94] and more than 35 European Late Pleistocene spotted hyena skulls (mainly grown up individuals, but also few sibling and cub skulls) [17], have yielded similar results. The sagittal crest is absent in infants and develops within juveniles after their teeth change and is strongly high in adults (Figure 2), which serves as the attachment for the massive bone crushing lower jaw musculature. Three different general skull shape variants similar in *C. c. spelaea* and in *C. c. crocuta* include (a) flat and (b) slight convex sagittal crest shapes (Figure 2). As demonstrated in Europe for the Late Pleistocene spotted hyenas, those types overlap and do not allow a clear separation of “races” (Figures 1(c) and 2). The third, (c) strong convex shape (only 5% of the skulls), was demonstrated for the Late Pleistocene and modern spotted hyenas to be rare and pathologic and partly the result of cranial bite damages caused by top predators in conflicts (other hyenas or lions or cave bears; see Figures 2 and 7) [17]. The best and most impressive damaged skull is from the Zoolithen Cave (Figure 7(b)), which historically [92] astonished scientists, because the brain case was not damaged, and the individual survived at least couples of days with strong skull bite trauma damage (two centimeter deep sagittal crest damage, Figure 7(b)). Full healing of such traumas resulted in high-convex sagittal crest shapes similar to those found at the open air site of Brühl-Spielwiesen (D) (Figure 7(b)) [48].

TABLE 1: 2.303 hyena and 1.373 lion bones of Late Pleistocene age from 105 studied cave and open air localities in Central Europe with Ice Age spotted hyena and steppe lion remains (details about the material, locality positions, and housing in collections can be found in the references).

Locality	Site type	Age	Hyenas (NISP)	Lions (NISP)	Bone assemblage (NISP)	References
Ahlen (D)	Open air loess, mammoth skeleton scavenging site	Weichselian (glacial)	Indirect by scavenging marks	0	Mammoth skeleton scavenging site	[55]
Alfter (D)	Open air loess on river terrace	Weichselian (glacial)	0	2	? unclear	[61]
Altussheim, Almendwiesen (D)	Open air loess on river terrace	Weichselian (glacial)	1	1	562	[61]
Altussheim, Eichelgarten (D)	Open air loess on river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Altussheim, Silzwiesen (D)	Open air loess on river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Altrip, Neuhofener Altrhein (D)	Open air loess on river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Bad Köstritz (D)	Zechstein gypsum karst hyena den (prey depot and communal den)	Weichselian (glacial)	2	4	? unclear	[61]
Bad Kösen (D)	Open air loess	Weichselian (glacial)	0	1	? unclear	[61]
Bad Lauchstädt (D)	Open air loess	Weichselian (glacial)	0	6 (from an adult female individual skeleton)	? unclear	[61]
Bad Wildungen (D)	Open air loess on river terrace	Weichselian (glacial)	11 (and 15 coprolites)	0	233	[49]
Balve Cave (D)	Carboniferous limestone cave (cave bear den, hyena cub raising and communal den/overlapping Neanderthal, and Aurignacian camp site)	Eemian-Weichselian (interglacial, mainly glacial)	34	56 (2 skulls)	? unclear	[42, 65]
Baumann's Cave (D)	Carboniferous limestone cave (cave bear den, short time hyena den, ? temporary wolf den)	? Saalian-Eemian, mainly-Weichselian (interglacial, mainly glacial)	10	148	? unclear, half Million cave bear bones	unpublished
Berlin-Kreuzberg (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Beroun (CZ)	Open air river terrace	Weichselian (glacial)	0	1 (skull)	? unclear	[80]
Bilstein Cave (D)	Carboniferous limestone cave (cave bear den, short time hyena den, ? temporary wolf den)	Weichselian (glacial)	2	39	? unclear, many cave bear remains	[82]
Brühl (Koller), Schlangenwinkel (D)	Open air river terrace	Weichselian (glacial)	0	12 bones of a male skeleton	? unclear	[85]

TABLE 1: Continued.

Locality	Site type	Age	Hyenas (NISP)	Lions (NISP)	Bone assemblage (NISP)	References
Brühl, Spieswiesen-Ost (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Brühl, Spieswiesen-West (D)	Open air river terrace	Weichselian (glacial)	8 (2 skulls)	4	1.255	[61]
Brühl (Koller), Rheingewann (D)	Open air river terrace	Weichselian (glacial)	1	3	511	[61]
Burgtonna (D)	Travertin	Eemian (interglacial)	1 (unclear amount)	3 (unclear amount)	? unclear	[61]
Bochum (D)	? Open air river terrace	? Weichselian (glacial)	0	1 (skull)	? unclear	[61]
Bottrop (D)	Open air river terrace (hyena communal den, partly cub raising den and prey depot)	Weichselian (glacial)	50	26 (and one trackway)	?, about 3.000 bones, many of hyena den origin (especially woolly rhinoceros)	[48, 61]
Deutmecker Cave (D)	Carboniferous limestone cave (hyena den)	Weichselian (glacial)	2	0	? unclear	[65]
Edingen (Brühl), Edinger Ried (D)	Open air river terrace	Weichselian (glacial)	2 (skulls)	2 and 8 bones of a male skeleton, including skull	1.111	[85]
Flörsheim (D)	Open air loess on river terrace	Weichselian (glacial)	1	0	? unclear	unpublished
Fuchsluken Cavities Saalfeld (D)	Zechstein limestone karst cavities hyena den (cub raising and communal den)	Eemian-Weichselian (interglacial, mainly glacial)	218	9	1.035	[61]
Freiburg a. d. U. (D)	Open air loess on river terrace, most probably Middle Palaeolithic site	Weichselian (glacial)	0	13 (from an adolescent individual skeleton)	?	[63]
Geddin (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Genther Cave (D)	Upper Jurassic dolomite cave (cave bear den)	Weichselian (glacial)	0	1 (skull)	? unclear	[71]
Göttingen (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Grürmanns Cave (D)	Carboniferous limestone cave (hyena den)	Weichselian (glacial)	11	1	? unclear	[65]
Halle/Saale (D)	Open air loess	Weichselian (glacial)	0	1	? unclear	[50]
Haltern (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Heddesheim, Neuwiesen (D)	Open air river terrace	Weichselian (glacial)	0	2	? unclear	[61]
Hermann's Cave (D)	Carboniferous limestone cave (cave bear den)	Weichselian (glacial)	0	47 (one skull, two individual skeleton remains)	? unclear, many cave bear bones	[76]

TABLE 1: Continued.

Locality	Site type	Age	Hyenas (NISP)	Lions (NISP)	Bone assemblage (NISP)	References
Herne (D)	Open air river terrace	Weichselian (glacial)	1	0	? unclear	[47]
Herten-Stuckenbusch (D)	Open air river terrace	Weichselian (glacial)	0	2	? unclear	[61]
Hohenmölsen (D)	Open air loess	Weichselian (glacial)	1 (skull)	0	? unclear	[50]
Hohle Stein Cave (D)	Carboniferous limestone cave (hyena prey depot)	Weichselian (glacial)	1	1	35	[65]
Holedeč near Žatec (CZ)	?	Weichselian (glacial)	0	2	? unclear	[80]
Hostím (CZ)	Open air river terrace	Weichselian (glacial)	0	4	? unclear	[80]
Huttenheim-Huttenheimer Kammer (D)	Open air river terrace	Weichselian (glacial)	0	3 and 37 bones of one lioness individual skeleton including skull	? unclear	[85]
Huttenheim, Sandfeld (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Johannes Cave (D)	Carboniferous limestone cave (hyena prey depot)	Weichselian (glacial)	3	2	31	[65]
Karlsruhe, Neureut (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Keppler Cave (D)	Carboniferous limestone cave (cave bear den)	Weichselian (glacial)	0	33	? unclear, many cave bear remains	[65]
Ketsch, Kreuzwiese (D)	Open air river terrace	Weichselian (glacial)	2 (skulls)	1	447	[61]
Ketsch, Hohwiesen (D)	Open air river terrace	Weichselian (glacial)	0	2	? unclear	[61]
Kleinbesten (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Königsau (D)	Open air river terrace (hyena den/overlapping Neanderthal camp site)	Weichselian (glacial)	13 (skull)	2	? unclear	[50, 61]
Körbisdorf (D)	Open air river terrace	Weichselian (glacial)	0	4	? unclear	[79]
Körbiskrug (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Koněprusy Cave (CZ)	Carboniferous limestone cave (hyena prey depot den)	Weichselian (glacial)	12 (25 coprolites, 114 bones from individual skeleton)	23	611	[38]
Kreuz Cave (D)	Carboniferous limestone cave (unclear site, ? cave bear den)	? Weichselian (glacial)	0	2	? unclear	[65]
Lahntal Cave (D)	Karst cave (cub raising den)	Weichselian (glacial)	82	0	13	[65]
Lampertheim, In der Tanne (D)	Open air river terrace	Weichselian (glacial)	0	2	? unclear	[61]

TABLE 1: Continued.

Locality	Site type	Age	Hyenas (NISP)	Lions (NISP)	Bone assemblage (NISP)	References
Lampertheim, Lüderitzbucht (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Lichtenau, Hasenkopf (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Lipperode (D)	Open air river terrace	Weichselian (glacial)	1	0	? unclear	[47]
Martins Cave (D)	Carboniferous limestone cave (cave bear den, hyena cub raising and communal den, wolf den)	Weichselian (glacial)	147	17	16 (real amount unclear), many cave bear remains	[65]
Medvedia Cave near Liptovský (Sk)	Limestone cave (cave bear den)	Weichselian (glacial)	0	Skeleton of a subadult	? unclear	[86]
Minice (CZ)	?	Weichselian (glacial)	0	1	? unclear	[80]
Mücheln (D)	Lake	? Eemian/ Weichselian	0	1	? unclear	[61]
Neumark-Nord Lake 1 (D)	Lake, forest elephants at a graveyard surrounded by Middle Palaeolithic camps	Eemian (interglacial)	6 (4 coprolites)	4 (and 172 bones from ill lioness individual skeleton)	Many hyena/lion scavenged elephant carcasses	[56, 84]
Niederlehme (D)	Open air river terrace	Weichselian (glacial)	1	7	? unclear	[61]
Oberneissen Cave (D)	Karst cave (cub raising den)	Weichselian (glacial)	14	0	? unclear	unpublished
Oberröblingen (D)	Open air loess	Weichselian (glacial)	0	1	? unclear	[61]
Oberrohn (D)	Open air loess	Weichselian (glacial)	0	1	? unclear	[61]
Otterstadt, Altrhein-Süd (D)	Open air river terrace	Weichselian (glacial)	0	2	? unclear	[61]
Otterstadt, Altrhein-Nord (D)	Open air river terrace	Weichselian (glacial)	0	3	? unclear	[61]
Otterstadt, Waldwiesen (D)	Open air river terrace	Weichselian (glacial)	0	3	? unclear	[61]
Osteroden (D)	Zechstein gypsum karst hyena den (type unclear)	? Weichselian (glacial)	1	0	? unclear	[50]
Perick Caves (D)	Carboniferous limestone cave (hyena cub raising and communal den)	Weichselian (glacial)	147 (5 skulls)	59	373	[10, 62]
Petershagen (D)	Open air river terrace	Weichselian (glacial)	0	1	Woolly rhinoceros skeleton, unscavaged	[61, 88]
Pfefferburg Cave (D)	Carboniferous limestone cave (hyena den, cave bear den, ? temporary wolf den)	Weichselian (glacial)	37 (and 8 coprolites)	2	31 (real amount ? unclear)	[65]
Phoeben (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]

TABLE 1: Continued.

Locality	Site type	Age	Hyenas (NISP)	Lions (NISP)	Bone assemblage (NISP)	References
Praha-Podbaba (CZ)	Open air river terrace	Weichselian (glacial)	0	16 (from two individual skeletons)	? unclear	[80]
Praha-Košíře (CZ)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[80]
Praha-Libeň (CZ)	Open air river terrace	Weichselian (glacial)	0	6	? unclear	[80]
Questenberg (D)	? unclear	? Weichselian (glacial)	1	0	? unclear	[50]
Rösenbeck Cave (D)	Carboniferous limestone cave (hyena communal and cave bear den)	Weichselian (glacial)	83 (5 skulls)	0	? unclear, many cave bear remains	[17]
Selm-Ternsche (D)	Open air river terrace	Weichselian (glacial)	3	0	? unclear	[47]
Siegsdorf (D)	River branch, river terrace site	Weichselian (glacial)	(3 coprolites)	62 bones of one male individual skeleton including skull	Mammoth bull carcass scavenging site	[75]
Speyer, Deutschof (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Svobodné Dvory near Hradec Králové (CZ)	? open air	Weichselian (glacial)	0	1	? unclear	[80]
Sewecken-Berge Quedlinburg (D)	Triassic gypsum karst hyena den (prey depot and communal den)	Eemian-Weichselian (interglacial, mainly glacial)	115 (1 skull of cub)	17	660	[52, 61]
Senzig (D)	Open air river terrace	? Weichselian (glacial)	0	1	? unclear	[61]
Sloup Cave (CZ)	Carboniferous limestone cave (hyena den, cave bear den, ? wolf den)	Weichselian (glacial)	85 (2 skulls)	4	52	[40]
Sophie's Cave (D)	Jurassic limestone cave (hyena cub raising and communal, cave bar, and wolf den)	Weichselian (glacial)	1	2	6, many cave bear remains (often carnivore damaged)	[45]
Speyer, Binsfeld-Südost (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Srbsko Chlum-Komín Cave (CZ)	Carboniferous limestone cave (hyena prey depot and commuting den)	Weichselian (glacial)	366 (from 6 individual skeletons, including cubs, 4 coprolites)	Two individual skeletons: 149 bones from an adolescent ill lioness, and 107 bones of a juvenile	2.947 (mainly Przewalski horse remains)	[39]
Teufelskammer Cave (D)	Carboniferous limestone cave (hyena den, cave bear den, ? temporary wolf den)	Weichselian (glacial)	71	1	97	[41]
Thiede (D)	Zechstein gypsum karst hyena den (prey depot and communal den)	Weichselian (glacial)	30 (1 skull of adult)	14	120 (even more, unclear amount at this stage)	[67]

TABLE 1: Continued.

Locality	Site type	Age	Hyenas (NISP)	Lions (NISP)	Bone assemblage (NISP)	References
Türmitz (CZ)	Open air loess	Weichselian (glacial)	2 (1 skull)	2	? unclear	[17]
Ústí nad Labem (CZ)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[80]
Výpustek Cave (CZ)	Carboniferous limestone cave (hyena den, cave bear den, ? temporary wolf den)	? Eemian/ Weichselian (interglacial/ glacial)	236 (3 skulls, one individual skeleton)	36	? unclear	Unpublished, skeleton in [39]
Wanne (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Westeregeln (D)	Zechstein gypsum karst hyena den (prey depot and communal den) and overlapping Neanderthal camp site	Weichselian (glacial)	84 (10 skulls, and 20 coprolites)	12	488	[51, 61]
Wildkirchli Cave (Ch)	Limestone cave (cave bear den)	Weichselian (glacial)	0	23	?, many cave bear remains	unpublished
Wiesental, Allmendweg (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Wiesental, Viehweg (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Wilhelms Cave (D)	Carboniferous limestone cave (hyena cub raising and communal den)	Weichselian (glacial)	169	15 (sibling skeleton remain)	126	[65]
Wörth, Geisbögel (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Wörth, Rheinanlagen (D)	Open air river terrace	Weichselian (glacial)	0	1	? unclear	[61]
Wüste Scheuer Abri (D)	Zechstein limestone abri/small cavity	Weichselian (glacial)	27 (1 skull)	0	61	[54]
Zechovice near Volyně (CZ)	? open air Loess	Weichselian (glacial)	0	1	? unclear	[80]
Zoolithen Cave (D)	Jurassic limestone cave (hyena cub raising and communal, cave bar, and wolf den)	Saalian to Eemian/ Weichselian (interglacial/ glacial)	207 (2 skulls)	229 (9 skulls)	Few bones, mainly damaged cave bear bones in unclear amount (about half Million cave bear bones)	[43, 44]

3.4. Ontogeny and Sexual Dimorphism. The ontogeny in *C. c. spelaea* was best known only from its teeth, which were determined with milk, cub, and adult teeth of all jaw positions by Reynolds 1900 [19]. Here, the ontogenetic stages are demonstrated for the skull with three stages, (a) sibling with milk dentition, (b) cub with fully changed permanent teeth, (c) and adult with already worn teeth (Figure 2). Also compiled are skeletons in sibling (composite skeleton) and adult ages (individual skeletons, Figure 1(d)) from Czech Republic caves. From some caves milk teeth and dentition such as a few rare brain cases and nearly complete skulls are figured [19, 24, 26, 29, 32, 37, 39, 41, 45, 51]. Often postcranial sibling and cub remains were misidentified in overlapping

hyena/cave bear dens, because their bones look very similar, and also the brain cases. Postcranial bones have been figured from a few caves and open air sites of Europe [41, 45, 51], because often those are strongly damaged and remained often unrecognized with fragments in the prey bone material. The sexual dimorphism in modern [94–97] and Pleistocene hyenas [17, 89, 91] in general is well known with the larger females, whose statistics are presented for several caves of Germany and Czech Republic [45], whereas in many cases the sex identification remains unclear, especially if the site is not well-dated to be interglacial (smaller forms) or glacial (larger forms), or in the close overlap of small females and larger males.

3.5. Cannibalism. The documented and illustrated record of bone damage in the Late Pleistocene spotted hyenas is recently much better [59] than the modern record. There are two types of bone damage: (a) cracked bones, which even fit, are demonstrated best for the Srbsko Chlum-Komín Cave (CZ) [41] where an old hyena carcass in the den cave itself was consumed and crushed into pieces (Figure 3(b)); (b) chewed and nibbled bones with many bite marks, especially at longbones, and cracked lower jaws are more typical at communal and birth den sites [39–43, 51]. At cave sites, postcranial hyena remains are more common, whereas cranial remains (especially skulls) are more represented at open air sites (e.g., Bad Wildungen, Bottrop, Upper Rhine Valley sites, Westeregeln, and others) [48–56], which is similar to some modern spotted hyena open air dens in Africa [94–96]. Hyenas dens contain similarly damaged bones (similar damages as their prey bones). The removal of the lower jaws of their own species skulls was only possible due to breakage of the jugal arches and breakage of the jaws behind the last teeth; therefore lower jaws are very often found without the ramus and skulls without jugal arches [17, 59, 97, 98], which is similar to damage on lion or cave bear skulls. Scavenging is reported in all age classes from several cave dens, whereas even infant and cub remains (cranial and postcranial) very often show patterns of cannibalism damage, similar to that on juvenile remains from a modern African spotted hyena den [39]. The common kills especially in siblings [99] are after new studies of modern spotted hyenas not related to the maternal rank and not correlated with cub survival in the modern spotted hyena [100]. The damage exhibited of their own species longbones is similar to other carnivores (lions, wolves) and also to cave bears [61].

3.6. Den Types. There are three different Late Pleistocene types of dens in Europe to distinguish based on (A) landscape morphology (Figures 7 and 8): (a) cave dens, (b) gypsum/limestone karst open air dens, and (c) river terrace/loess open air dens [39, 51, 52, 54–56] which are mapped in detail in the case study area of Germany/Czech Republic in both, lowlands and mountainous regions (Figures 1 and 8). Hyena population structure and bone assemblage analyses (both after NISP) suggest that those morphotypes of dens are comparable to modern African spotted hyena den types similarly based on the (b) ethology and demography of populations [101–104], which is more difficult to compare to palaeopopulations and their fossil record. Three main types are distinguished in the Late Pleistocene of Europe (Figure 8): (a) birth/natal den (similar to Africa [103]: sibling bones/milk teeth, abundant “nibbling sticks”, and few prey fauna remains which are strongly damaged, e.g., [37, 43, 49, 53]); (b) communal den (similar to Africa and most common den type [24, 35, 39, 41, 43, 45, 53, 54]: cub and mainly adult to senile hyena bones, often cannibalistic damaged, prey remains more fragmented and chewed, and abundant coprolites for den marking); (c) prey depot den (mainly/only adult remains and even articulated skeletons, abundant prey remains partly body parts in articulation and less bone damage, and few

coprolites), which is more typical type of the Late Pleistocene cold period and cave-rich regions of Europe [34, 40].

3.7. Prey Remain “Bone” Accumulators. Hyenids of the Miocene to Early Pleistocene (including different ecomorphs: bone crushing, hunting, civet-like, and others) seem to have started to develop bone accumulations (especially *Crocota*) with bone damage due to prey import to dens (and less single bones). The earliest European *Crocota* records date back to the Pliocene [102, 103, 105] with few sites known from the Early [106–108] and Middle Pleistocene [109]. Only bone-cracking ecomorph hyenids persisted in Europe to the Late Pleistocene. The most famous European Early Pleistocene Untermassfeld (D) site with a *Pachycrocota* population [108]—here identified as a very typical “hyena open air and bone accumulation den site” on a river terrace position (high amount of *Pachycrocota* remains, coprolites, many chew-damaged prey bones, often leg bone overrepresentation), with possible local short-distance transport after the carnivore prey remain depositions—was even incorrectly interpreted as resulting “only by floods accumulated” bone assemblage, which demonstrate that open air communal hyena den sites are still often overlooked. As herein compiled, the best and most dense fossil record of large carnivores and their activities and bone assemblages is from the Late Pleistocene (Figure 8). To understand those fossil “carnivore bone assemblages” most bone taphonomy studies dealt more recent only with the question about “anthropogenic or carnivore bone assemblage identification” [110–116] but did not consider the palaeoecology of extinct hyenas and the complex cave bone taphonomy, especially in caves. Bone accumulations caused by modern spotted hyenas, to avoid conflict with lions and other carnivores and to feed their cubs at the den site, are studied in several small caves and open air locations in Africa in some cases at least by their NISP and MNI [96, 107–122]. In Europe there was not a standard to analyse hyena den prey bone assemblages, and often only single animal groups were published from sites and are listed without NISP and MNI reports [30], while more recent works include the prey bone quantitative analyses. These quantitative statistics allow a first general hyena den site (versus human site) identification, because, at most Late Pleistocene spotted hyena den sites, 10–35% of the bones are hyena remains [32, 54] (Figure 8). In a second qualitative/quantitative study, less the “classical bite mark analyses” [123, 124] supports a hyena den bone accumulation origin, as furthermore the “repeating bone damage stage analyses” [125–130], which is best made with elephant and rhinoceros remains [50, 57] and bone element abundance [126, 127] whereas the schlepp effect [129] (= selection of body parts at scavenging site and nonimportation of all types from prey body, such as vertebral columns) is included in such studies. Finally the general “damage degree” is important simply to distinguish human “kitchen rubbish” (= mainly bone fragments at sites), and “carnivore sites” (= abundant complete and partly articulated remains) [110–130].

3.8. Bone Damage Stages. Modern and Late Pleistocene spotted hyenas are “bone crushers” [22, 130] with their specialized bone cracking jaws and dentition [89, 131] (Figure 6). Remains of old aged individuals show crown damage or the loss of mainly the lower jaw premolar teeth (bone crushing teeth) and fully used incise teeth (bone nibbling teeth) which is demonstrated both for modern [132] and now for the Late Pleistocene spotted hyenas of Europe. There are two main groups of bones/prey types: (a) elephants and rhinoceros with unbreakable bones and (b) bovid, equid, cervid, ursid and antelope herbivorous, and carnivore bones which can be crushed by hyenas. For extinct elephant (*Mammuthus* [57], *Palaeoloxodon* [58]) and rhinoceros (*Coelodonta* [50]), in each taxon, three bone damage stages were presented being nearly identical as those of similar hyena butchering/decomposition techniques on the largest prey and of similar spongy filled bone structure of “uncrushable massive bones.” In other Late Pleistocene megafauna mammal prey, those stages are not yet well distinguished, such as for horses, bovids, or cervids, but typically more abundant distal leg elements were left often untouched at den sites [53–55, 133, 134], similar to those known from modern spotted hyena dens [125, 126, 129]. At some sites even those distal leg bones (metapodials and phalanges mainly) of deer, horses, or steppe bison were also crushed as best documented at the Perick Caves (D) hyena den [134–136] or Srbsko Chlum Komín Cave (CZ) [41] and Fuchsluken Cavity (D) [137]. Only two stages are described for modern bone shafts and bone fragments of cracked longbones. Also the cervid bones were much more easier to crush into pieces (similar as antelope bones [136]), and, therefore, longbones are mostly present fragmented and not chewed at Late Pleistocene spotted hyena den sites all over Europe. The nonelephant/rhinoceros bones were finally often used as “nibbling sticks” [130–136].

3.9. Nibbling Sticks and Play Bones. The so-called “nibbling sticks” are very typical at birth dens and less common at communal dens, though absent at prey storage dens [39]. These are any kind of bone fragments (mainly nonelephant/rhinoceros bones) which were first unipolar, then bipolar chewed mainly by siblings and cubs for teething purposes. They are best represented at the Nad Kačákem Cave (CZ) [39] where more than 60 strongly chewed bone fragments have been found. These nibbling sticks include less mammoth [57] and rhinoceros [50] and are known from other Late Pleistocene spotted hyena cave and open air den sites as useful for hyena den identification but are not yet published well from modern sites, however. Besides those, play bones are present, especially of elephants [57, 58], which are pieces mainly from the pelvis and scapula (= “Neanderthal pseudo hand axes” [57]) or femur joint heads of young elephants [58] which were also strongly chewed over longer periods.

3.10. Den Marking by Faeces. The fossil record is problematic, because coprolites have not been recovered or crumbled to “dust” over the centuries in many collections. Hyena dens and territorial boundaries are marked by extant hyenas [138] and

were marked in the Late Pleistocene as documented best at communal den sites [60, 139]. In some European caves hyenas trampled even complete phosphatic horizons, historically described for Lindental Cave [14] or König-Ludwigs Cave (D) [9], whereas in Srbsko Chlum-Komín Cave (CZ) the phosphate pieces built a high percentage of the sediment [41]. At Czech Sloup Cave, Srbsko Chlum-Komín or Koněprusy Cave [40–42], and French caves (e.g., Rochelot Cave [34] and others) or Spanish caves [140], coprolites have been reported to be partly abundant, whereas also at the open air site Westeregeln (D) two faecal places with coprolite concentrations were documented at an open air communal gypsum karst den within the sinkhole [60]. An overview of the few surviving material has been published for the German and Czech hyena den and carcass scavenging sites whereas the different typical hyena shaped pellets built aggregates (Figure 3(c)), which are well compared to modern spotted hyena excrements [60]. Modern hyenas mark their dens and territory against other clans and even lions [138, 139] which must be expected for the Pleistocene record, too. Such early cemented coprolites can survive even water transport [141], especially if cemented and encrusted, for example, by caliche, and even survive salt water as reported from the North Sea [142]. Extractions of pollen from such excrements were used to reconstruct the vegetation and palaeoenvironment [143], but those studies did not take into account that these plant remains are not consumed by hyenas and seem to result more from intestine/inner organ feeding by hyenas of their prey. Therefore, the pollen from hyena faeces can completely reflect the diet of hyena’s prey (= last plant food of the prey), which itself was selective in plant feeding [60]. To reconstruct “vegetation and landscape” based only by this is problematic, but in combination with hyena prey analyses, it might help to understand the prey of hyenas using their coprolites based on pollen and bone fragment DNA analyses.

3.11. Horse and Donkey Hunters. The main prey found at hyena den sites all over Europe is from horses. According to the latest revision of the Late Pleistocene European horse “*Equus germanicus* Nehring, 1884” based on those from Westeregeln (D) hyena den, it is determined that they are synonymous to the modern small Przewalski horse *Equus caballus przewalskii* Poljakov, 1881 [53]. Even at the Sewecken-Berge (D) hyena den, the “unicorn holotype skeleton” was demonstrated to have been composed of Przewalski horse skeleton remains [54]. At this site hyenas hunted additionally a “larger horse” *Equus caballus* cf. *fossilis* (taxonomy still unrevised) within the Eemian interglacial times [54]. At several caves, including the Wookey Hole hyena den (GB) [13], horses are the most abundant prey. At den sites abundant teeth were found which resulted from the crushing of the thin-walled skulls and moderately massive lower jaws. Additionally, also as best documented at Rochelot Cave [34], bones at den sites are dominated by distal leg elements, which were found partly in anatomical connections (= leg import). The horse hunting specialization of the Late Pleistocene spotted hyenas is best and most impressively documented at the Srbsko-Chlum-Komín Cave (CZ), where 51% of the

NISP are small caballoid *E. c. przewalskii* horse bones (more than 1,500 bones). For modern spotted hyenas, equid (zebra) predation is well documented at two African hyena den bone assemblages of the Amboseli [119] and Syokimanu [96] dens sites (23% and 13% zebras) and zebras can reach up to 70% of hunted remains [133]. Within the Srbsko-Chlum-Komín Cave, remains of three foetal horses (one nearly complete foetus skeleton) suggested that hunting time occurred in the spring time; therefore mother horses were imported as carcasses to the den [133]. The Late Pleistocene record there indicates that the hunt was targeting mainly grown up horses (92%), which is similar to zebra hunting in African hyenas [133]. The hunting of horses does depend on the different Late Pleistocene landscapes (Figure 8(b)), as they are more abundant in mammoth steppe environments but can be highly abundant in valleys of mountainous regions where there are much fewer cave bears as a possible food (e.g., Bohemian Karst [39]). This again is similar to modern hyenas, which also depend on landscape differences (woodland, mountain, and savannah) for different prey, and therefore prey abundance can be very different in modern spotted hyena bone accumulations [59, 88, 95–97, 106, 115, 117–122, 133, 144]. Late Pleistocene donkeys *Equus hemionus hemionus* were also targeted mainly in the steppe environments, as demonstrated well by two sites which have their remains in the hyena dens, the Fuchsluken Cavity (D) [137], and Agios Georgios Cave (Gr) [29]. In other caves and open air dens of Europe, these donkeys are generally rarer in the hyena den bone assemblages (1–3%).

3.12. Bovid Hunters or Scavengers. The steppe bison *Bison priscus* was targeted in the cold periods only in some areas or periods by Late Pleistocene spotted hyenas, especially where hyena dens were abundant, but cave bears (and elephants) were rare such as in the Thuringian Karst [56, 137]. There are only few examples where steppe bison hunting specialization developed as reaction to cave bear/mammoth prey absence or rareness, such as at Fuchsluken Cavity (D) [137]. At this hyena den, a high abundance (32% NISP) of bovid, mainly steppe bison, is unique for the German and Czech hyena den record. In Camiac Cave (F), the steppe bison (and/or bovid) remains were calculated to represent 39% of the prey fauna [27]. Also in Rochelot Cave (F), bovids were the second abundant prey remain [34]. In Italy San Teredo Cave (Sicily) even higher amounts (up to 50% NISP in some layers) were from bovids [37], also indicating a specialization there. Generally, steppe bisons are represented in similar abundance as horses in the mammoth steppe bone assemblages and are more rare in boreal or mountain forest hyena den bone assemblages (Figure 5(b)). The less important role (few NISP) of steppe bison at most hyena den sites in lowland den sites (e.g., Westeregeln, Bottrop) also indicates a competition/prey overlap, probably with the Late Pleistocene steppe lions and wolves, which were the active hunters, hyenas more the scavengers (Figure 8(b)). This suggestion is also supported by rare bison NISP amount at the Srbsko Chlum-Komín Cave hyena prey depot, where as in this most large European hyena den bone assemblage (NISP = 3,695) only few steppe bison remains (2% of NISP) are found [41]. Also, in the same

landscape at the hyena prey depot of Koněprusy Cave, only 6% of the bone assemblage material was from the steppe bison [40]. The habitat variability in mountain regions with limited cave bear/mammoth seems to have determined either the bovid or equid hunting specialization—and logically those had to be hunted in higher amounts to reach the nutrition biomass. This explains the best high bovid/equid prey percentages at both sites (Fuchsluken Cavity and Srbsko Chlum-Komín Cave). This is similar to African lions, which also specialize in hunting of buffalo in wetland areas (e.g., African Amboseli hyena den) [119], whereas Canadian wolf clans target woodland bison in mountain woodland regions of Canada [137, 145]. The same hyena/lion/wolf prey role occurs, though much less frequently, with *Bos primigenius* mainly in warm age periods. Scavenging is comparable to the modern spotted hyenas scavenging in “elephant-free” areas as documented in two modern African hyena den bone assemblages of the Amboseli [119] (buffalo/domestic cattle = 6%, wildbeest = 33%) and Syokimanu [96] dens sites (domestic cattle = 30%, wildbeest = 7%) [133].

3.13. Deer Scavenges and Shed Antler Collectors. Fast running cervids were not a main hunted food source for slow spotted hyenas (Figures 8(b) and 8(c)) similar to that gazelles are not the main hunted (but scavenged) prey in modern African spotted hyenas [59, 88, 95–97, 106, 115, 117–122, 133, 144]. Their rarity in the bone record of all studied hyena den bone assemblages must be interpreted carefully, because their bones are easy to crush and to swallow for bone collagen use. For the Perick Caves, the *Megaloceros giganteus* bone record demonstrates that cranial remains and distal leg elements dominate the bone record at den sites [136], as represented at the Sewecken-Berge [54] and Fuchsluken Cavity [137]. At all sites studied, the record of red and giant deer is always limited and bones are highly fragmented, whereas the remains of reindeer are variable in amounts and preservation, especially at hyena dens/overlapping human camp sites [53]. Compared to bovids and equiids or rhinoceroses, isolated teeth of the hunted cervid prey are more useful to estimate the MNI. Even with this, cervids are rarely represented by the tooth record at the dens. Obviously, cervids (*Megaloceros*, *Cervus*, *Dama*, and *Capreolus*) were not an important or main food source for the Late Pleistocene spotted hyenas at all (e.g., nearly absence even in boreal forest den sites like Srbsko Chlum-Komín Cave [41], where reindeer remains were possibly imported by wolves). Very interesting and only typical for hyenas in the European Late Pleistocene is the collecting of shed deer antlers, which is partly comparable to collected horns of gazelles found at African den sites [96]. The study of all hyena den antler records from Late Pleistocene dens in central Europe indicates that the importation of antlers (1–10 antlers only on each den site) by hyenas always left similar damage marks to the remains: the base with strong bite scratch marks at the chewed end and those on antler fragments of older individuals. The rough lower attachment part was never chewed, because it could have damaged the tooth meat.

3.14. Woolly Rhinoceros Carcass Decomposers. Only a single woolly rhinoceros carcass has been found in Petershagen of northern Germany and was found in articulation untouched by carnivores [146]. There is one scavenged skeleton from the Krölpa (D) open air gypsum karst scavenging site [56] and most probably another skeleton from the Bad Wildungen hyena open air loess den [51]. Both carcasses demonstrate carcass decomposition stage 2 (of 3), where the anatomical context is moderately to mostly destroyed, and parts have been already removed. In most hyena dens sites the bones are isolated or body parts are partly in anatomical context (mainly legs). The damage on rhinoceros bones of the Late Pleistocene is the best “hyena den marker” at all, because bones found at dens or open air scavenging sites follow a consistent damage pattern [50]. *Coelodonta antiquitatis* skulls (e.g., Koněprusy Cave, Srbsko Clum-Komin Cave, Krölpa) [39–41, 56] are documented to have been damaged similar as cannibalistic damaged hyena skulls (cracked jugals and ramus damage). In situations such as communal den sites, the skulls exhibit even greater damage, and only teeth are left, and in several cases were even compiled in dentition rows (e.g., Westeregeln [53], Sewecken-Berge [54]). There and at open air carcass scavenging sites, hyenas left excellent examples of brain case opening on calf to adult individual skulls (Bad Wildungen [51], Selm-Ternsche [50], and Krölpa [56]). All over Europe, Late Pleistocene spotted hyenas caused three main and similar bone damage stages on the pelvis, scapula, and longbones. Such are documented in greater amounts at open air dens (Bottrop [50], Bad Wildungen [51]) or cave den sites (Lindenthal Cave [14], Sveduv Stůl Cave [24], Teufelskammer Cave [43], Balve Cave [44], Srbsko Chlum-Komin Cave [41], Koněprusy Cave [40], or Sloup Cave [42]). With the carcass scavenging sites (carcass decomposition stages 1–3), a butcher technique for carcass decompositions on the second largest hyena prey is now demonstrated, which only is hyena-related. This has not been studied yet on modern African rhinoceros carcasses. Within the rhinoceros carcass butcher/decomposing technique, hyenas moved body parts to the den sites to avoid conflicts with lions/wolves. This is nearly identical to the carcass decomposition and bone damage stages of elephant bones (mammoth, forest elephants). At many cave sites, the woolly rhinoceros was imported abundantly which indicate that these were important food sources for meat and bones (e.g., Teufelskammer Cave [43], Bottrop [50], Bad Wildungen [51], Westeregeln [53]) being mostly on second position within the NISP (e.g., Lindenthal Cave [14], Wookey Hole [15], and Sewecken-Berge [54]) (Figures 9(b) and 9(c)), also as result of robustness of the uncrushable bones.

3.15. Woolly Mammoth Carcass Butcher Technique. The decomposition of extinct and extant elephants (*Loxodonta* [46], *Palaeoloxodon* [58], and *Mammuthus* [57]) by modern and Late Pleistocene spotted hyenas is now being studied in detail. Lions and hyenas feeding on elephant carcasses overlap (Figure 9(c)) but are recognized only once in the initial stage 1 of carcass decomposition of a woolly mammoth at the Siegsdorf (D) bull carcass (intestine/inner organ, trunk, and feet feeding [57, 58, 147]). The destruction of the bones

is similar to rhinoceros, because of similar prey size and similar bone structure. In elephant and rhinoceros, the bones are filled by spongiosa and are nearly unbreakable, even for hyenas [57, 58]. They only can chew their longbones and larger bones starting from the soft distal joints. The elephant feeding starts similarly in both top predators quite often on the inner organs/intestines, which body cavity they reach often over the anus [148]. Canine bite scratches on the inner side of the thoracic/lumbar vertebral columns on three *Palaeoloxodon* skeletons of Neumark-Nord Lake 1 demonstrated that top predators went into the body cavity eating from inside [58], which is even known from modern hyenas and lions in documentary films [149]. This is simple to explain, because the very thick skin is even hard to cut by top predators. The skin at the anus is thin and feeding from behind allows to consume intestines first. Also the trunk is initially eaten in elephant carcasses or the feet mainly by hyenas which was monitored at an African elephant carcass [148]. There are three main decomposition stages on elephant carcass documented in the fossil record. Hyenas are the only predators that start the second stage on elephants, especially on the legs. With this, the carcass is damaged and demonstrates why there are only few mammoth/forests elephant skeleton remains found complete in Europe. Exceptions are carcasses which were found in shallow lakes or river branches partly covered by water, such as at Neumark-Nord Lake 1 (several skeletons of *P. antiquitatis* [58]). The best example of initial feeding on *M. primigenius* is the large bull from Siegsdorf (D) [57]. The Ahlen (D) or Klinge (D) skeletons are further damaged (decomposition stage 2 [57]), whereas in all there is also typical damage to the skull, which is thin-walled and spongy-like in construction and easy to damage by hyenas. The final damage of the larger bones happened at communal or birth den sites where mainly bones of mammoth calves to subadults were found [57], simply a reason of transportation selection of smaller animal and body parts of less weight (= schlepp effect [129]). In some cases hyenas fed on mammoth remains, which Neanderthal humans left at cave camp sites (Weinberg Caves [149]), or stole fragments which they imported to their dens (Perick Caves [57]). The greater amount of calf remains cannot only be simply interpreted as “hunted mammoth calves” by hyena clans, which indeed cannot be excluded. Modern lions (or even Late Pleistocene subspecies) are the more successful elephant calf killers [148]. In all bone accumulations at hyena dens mainly teeth and bones from mammoth calves and subadults have been found, whereas their percentage in the NISP is always not that high (Figure 9(b)), but the body mass and weight are indeed much higher. Obviously, elephants were lowland inhabitants, and therefore they are very rare or absent in boreal forest hyena den cave faunal assemblages (Bohemian Karst [39], Thuringian Karst [137], and Sauerland Karst [57]), because of seasonal migration within the valleys of the mountain slopes.

3.16. Cave Bear Scavengers in Caves. The scavenging of cave bears (and bone damage) was initially believed to be a result of “cannibalism within cave bears” [11, 52]. This can only be understood by including megafauna quantitative and

qualitative analyses and the hyena and lion (also wolf) bone record, including their taphonomy and ethology [61]. Many arguments against this “bear cannibalism” hypothesis have been published, such as the tooth morphology changes as adaptations to plant feeding (increasing of enamel cones and molar tooth size [150]); the nitrogen isotope record demonstrating a fully-herbivorous cave bears in the Late Pleistocene [151]; similar damage patterns left on cave bear skulls, jaws and long bones mainly, in addition to puncture and marks and chewing present on cave bear bones in every cave bear den of Europe [61]. The puncture marks were especially misinterpreted to have resulted from “noncarnivorous” cave bear canines, with round-oval holes in cave bear cub longbones also misidentified as “Neanderthal pseudo-bone flutes”—but those results are certainly from the molar crushing teeth of hyenas [61]. Hyenas were unable to crush cave bear cub femorae and longbones into pieces, because those were not calcified enough, and only subadult to adult longbones were crushed successfully to pieces in larger amounts in some caves [61]. The first evidence of hyena impacts on cave bear populations was published in 2005 based on bone taphonomy studies and full analyses of overlapping hyena and cave bear dens of the Perick Caves [152]. Still after this, cave bear researchers believed in “bone consumption” of cave bears, which was again incorrectly published for the Oase Cave (Ro) [153], where the hyena skull [17] find was first overlooked (also overlapping hyena/cave bear den). Hyena presence explain also there the large amounts of bone fragments (up to 21% of cave bear bones damaged). Hyenas specialized without a doubt in boreal mountain forest regions all over Europe, where cave bear populations were well represented in possibly higher densities as believed (“one cave bear family per cave” [150]). Evidence for their carcass feeding (possibly also killing of cubs = overlap with lion prey; Figure 9(c)), as a result of absence or rareness of the mammoth and its steppe megafauna abundance variability (especially horse/steppe bison) in those landscapes, is demonstrated for several caves such as best illustrated for the Perick Caves [152] or Zoolithen Cave [45].

3.17. Neanderthal Human Exhumers and Scavengers. There are two obvious examples where Late Pleistocene spotted hyenas must have exhumed and eaten Neanderthal human carcasses. The first convincing record is from the Rochelot Cave (F), where some teeth and cracked longbone fragments were found in a classical hyena den between Eemian interglacial equiid/bovid prey remains [34]. The interpretation of the nonhuman camp or burial in smaller caves documents the consuming of humans by Late Pleistocene spotted hyenas [154]. Fractured bone remains of several Neanderthal humans found in the Divje Babe I Cave (Hr) interpreted to have resulted from human cannibalism [155] are herein reconsidered for several reasons. Firstly, the cave was obviously not a well studied hyena den (own observations on carnivore bone material). Secondly, the human longbone fragments which have no evidence of “hit marks” suggesting they result from hyena bone crushing activities. The most important argument comes from comparing modern human

bone material, which was exhumed from more than one meters in depth beside a hospital in Africa by spotted hyenas (unpublished Sutcliffe-modern hyena den collection in the BMNHL), where there is evidence for human body parts and crania imported into a small cave den. There, skulls were crushed in fragments similarly as all the long bones, and this material is a key for the understanding of hyenas scavenging on Neanderthals and humans/apes in general. Also, the Croatian Divje Babe I Cave is another overlapping hyena den/Neanderthal camp site. It is plausible that hyenas exhumed humans which were not deeply buried and left behind only crania pieces, teeth, and longbone fragments. The breakage patterns and selective presence of crania and longbone fragments correlate with the hyena den site of Rochelot Cave (F) and the modern African den sites, and therefore Neanderthals must have been on the list of the hyena prey, at minimum as carcasses. However, attacks on humans by these predators, especially on large portal caves where hyenas and humans occupied both of those, must be expected because both used those seasonally at the same or even different times, which complex situation has also been discussed for the overlapping hyena/Neanderthal site at Balve Cave (D) [44].

4. Late Pleistocene Steppe Lions

The lions of the Eurasian Late Pleistocene (Figures 4–6) were called historically “cave lions” because they were first found in the Zoolithen Cave (D) [5] and other caves in Europe. However, they were recently revised according to DNA [156, 157] studies to the Late Pleistocene steppe lion *Panthera leo spelaea* (Goldfuss, 1810). The holotype skull has composed lower jaws from other individuals [46]. Those Late Pleistocene steppe lions from the Eemian interglacial were smaller (e.g., modern males were nearly similar in size to Eemian males, which represent possibly even another warm period subspecies), but those of the Weichselian glacial were larger using the largest skulls [46, 79]. Similar to the modern African lions [77] the cold period males in the extinct species [77] are few larger [46, 77], which is also reflected in the skull record of Europe, whereas sibling to early adult skulls can not be attributed well to the sex (Figure 5).

4.1. Palaeopopulations over Europe. Lions were thought to be “rare” in the Late Pleistocene fossil record of Europe, but this was only because of a lack of research, mainly. In the past five years the addition of new unpublished material and revision of lion remains in Germany [46, 64, 66, 67, 83–86] and Czech Republic [62, 82] (1.373 bones, including remains of 9 skeletons) and new finds (4 skeletons) in Romania [61, 65] demonstrate “dens palaeopopulations” in the Late Pleistocene (Figure 3, Table 1) with a bone record ratio of 1 lion/3 hyenas. Some individual skeletons (Figure 3) and hundreds of bones have been described over the past years from Germany and Czech Republic, demonstrating more hyenas in the bone record, which does not reflect the real individual animal amounts because the mortality and taphonomy situation for both is different, especially in the cave dens. Lions were found

instead less at open air sites [62, 66, 67, 85] and are more abundant in cave bear or hyena dens [46, 61, 65, 82–84, 86] (Table 1).

4.2. Holotype Skulls and Skeletons. The recently rediscovered holotype skull of “*Felis spelaea*” was originally found in the Zoolithen Cave of Bavaria (D) [5]. The lower jaws from this skull are actually composed from different individuals, with one mandible from a female incorrectly attributed to the male skull [8]. The largest palaeopopulation (possibly including different subspecies) was found in the European Zoolithen Cave [46]. Also from this Zoolithen Cave, similar to as many localities in Europe, articulated skeletons are absent because of three reasons: (a) historically nonprofessional excavation and collecting, (b) rare lion cannibalism (except of cubs), and (c) transportation by floods (third position). Most recently, a fairly complete skeleton of an individual subadult lioness with braincase damage was described from the Weichselian glacial Srbsko Chlum-Komín Cave hyena den (CZ) [82] (Figure 4). Another skeleton with a more heavily modern damaged pelvic area (Figure 4) of another strong ill lioness was found within the Neumark-Nord Lake 1 open air elephant graveyard site dating to the Eemian interglacial (D) [61]. Remains of three glacial aged skeletons from the Uršilor Cave cave bear den (Ro) (Figure 4) [65, 84] are the most spectacular finds at all. Other glacial lion skeletons have been found at various German (Siegsdorf [77], Huttenheim, Edingen, Brühl [66]), and Czech (Praha-Podbaba [63]) open air river terrace sites. Further skeletons have also been reported in unclear taphonomic context from Spain (Arrikutz) [74] and Austria (Salzburg) [75]. The only known cub skeleton was found within a hyena den (Wilhelms Cave, D) and seem to have been imported as “hyena prey” or was killed by hyenas at their den site during prey stealing or cub killing purposes [85].

4.3. Ontogeny and Sexual Dimorphism. The ontogeny in *P. l. spelaea* was originally confusing and young individual material from the Zoolithen Cave was incorrectly attributed to a “cave tiger,” which was revised [46]. Cub individual remains are rare in contrast to hyenas and have only been found with a partial skeleton in the Wilhelms Cave (D) hyena den [85], which demonstrates that this animal was not a cave “inhabitant,” nor periodically “cave user,” but only a dweller (Figure 8). Skeletons are only of subadult to senile in age (Figure 4). The sexual dimorphism in modern [77, 158–160] and Pleistocene lions [46, 77] is well known best from the teeth [160], crania, but also in postcranial comparisons [66]. In contrast to hyenas, male lions are known to be larger based on data presented for several caves and open air sites of Germany and Czech Republic [46]. There, the sex identification remains often unclear in cubs/subadults, especially if the site is not well-dated to be interglacial (smaller forms) or glacial (larger forms) or in the close overlap of small females and larger males [46, 66, 77].

4.4. Steppe Lions as Cave Dwellers. Additional to the taphonomic and nitrogen isotope record, the fossil record data on lion remains from cave bear dens indicate that only subadult

to adult lion individuals died in the caves [46, 84]. Clearly the use of caves by lions can be excluded in comparison to the mortality of cave bears and hyenas (Figure 8) [6]. Late Pleistocene steppe lions were open environment inhabitants ranging in their territories from mammoth steppe to boreal forest environments, similar in ethology to their modern relatives in Africa [46, 66, 84]. Therefore, the historically named “cave lion” was recently renamed the “steppe lion” [8] according to DNA, taphonomic, and behavioural information.

4.5. Reindeer and Bison Hunters. Nitrogen isotopic studies on the Late Pleistocene steppe lions indicate that they seem to have switched to reindeer hunting at the end of the Late Pleistocene [161] as a result of extinction of the mammoth steppe megafauna and cave bears [158]. This is comparable to modern lions which typically hunt gazelles [158, 159]. Lions, as fast runners, seem to have specialized more in fast prey such as cervids (*Cervus*, *Megaloceros*, and *Dama*) or bovids (*Bos*, *Bison*) in the Late Pleistocene similar to the large wolf subspecies, possibly both hunting in packs. It must also be expected that the rare steppe bison/aurochs remains in most hyena dens reflect the prey competition with lions/wolves. As known in Africa, bovids are the main target of lions in many regions [158].

4.6. Mammoth and Forest Elephant Initial Feeders. Specialized predation on young-subadult elephants [162] cannot be demonstrated in the Late Pleistocene record of hyena den bone assemblages. At these sites the mammoth presence/absence depends more on the landscape morphology [57] (Figure 9(b)). Information of the lion's largest prey comes best from the fossil elephant carcass sites Siegsdorf (*M. primigenius* skeleton, glacial) and the Neumark-Nord Lake 1 site (*Palaeoloxodon* skeletons, interglacial). As documented in Africa, modern lions start to consume the trunk, and from the anus from where they eat the intestines of the body cavity finally from inside [58]. This is also well shown from modern hyenas and lions in documentary films [148] and a monitored *Loxodonta* carcass [147]. Modern hyenas feed on elephant carcasses at the killing site in the carcass decomposition stage 1 [147].

4.7. Cave Bear Cub Killers. In contrast to the Late Pleistocene spotted hyenas, the prey of the lions is much more difficult to reconstruct, because they did not [158, 159] accumulate prey or bone remains of their prey or do not leave consistently damaged bones. The theory about lions killing cave bears even in deep caves resulted from taphonomic studies, whereas convincing evidence has recently emerged from Uršilor Cave cave bear den (Ro, Figure 4) [61, 65]. Further evidence from taphonomic studies is demonstrated from several caves in the Sauerland Karst [86]. Similar results were found finally at the Zoolithen Cave with the largest steppe lion population found ever in a large cave bear den (about a half million cave bear bones), where a feeding specialization on cave bears was argued due to the absence of mammoth steppe fauna in mountainous regions [61]. The latest nitrogen isotope data

supports the cave bear hunting interpretation, whereas others even went further to declare that only “cubs” were a main food source [161]. More recent taphonomic studies at Sophie’s Cave support this. The hunting of cave bears by lions explains that cave bears hibernated as deep as possible in larger cave systems even in dangerous passages to protect themselves against lion attacks [46]. Hunting cave bears in the caves seems to have been done mainly by females. There are some larger cave bear dens in Europe (e.g., Keppeler Cave, Urşilor Cave, and possibly also Hermann’s Cave), where two third of the lion bone material belongs to females. This is a similar behaviour as in modern lions, where dominant lionesses hunt in packs [158, 159]. A pair or pack hunt by Late Pleistocene steppe lions in the caves must be expected.

4.8. Deathly Battles with Cave Bears. The lion bone record in caves might simply demonstrate that females were more easily killed by grown up cave bears during conflicts in the cave dens [65]. Interestingly the amount of overlap at hyena/cave bear den sites of the male/female ratio is opposite to that of lions (Bilstein Cave [83], Perick Caves [64], and Zoolithen Cave [46]) with only one third of the bones from female hyenas. Lions must have been unsuccessful sometimes while hunting in the cave (Figure 8(d)). There are three examples of lion skeletons which seem to be the result of lost fights: (a) Sloup Cave “skeletons” (at minimum 2) [62], (b) Urşilor Cave skeletons (at minimum 3, Figure 6), and (c) Zoolithen Cave [46] (unclear amount, but remains are from originally partially articulated skeletons [46]). The lion remains in bone-rich cave bear dens never exceed 1–3% of the total NISP bone amount [46, 61, 67, 83, 84]. This calculates to only one dead lion per 10,000 years at maximum, which suggests often successful hunting on the “hibernating” and easy to kill cubs over ten thousands of years. The aforementioned “normal mortality” in cave bears of Europe [163–165] does not exist; instead, the high mortality in cave bear cubs (also here Zoolithen Cave: Figure 8(a)) seems to be a combination of both: natural dying and predation mortality (Figure 8), which is demonstrated by the percentage of bite damaged cub bones, whereas most of the bite damages clearly are of postmortal times (e.g., chewed joints). Also the picture of the cave bears’ life and death was presented incorrectly [150], such as in the bone taphonomy (cave bears as “cannibals” [166]), by not taking the predators into any account in any cave bear population statistics/mortality analyses. However, because of the lack of modern lion/bear population overlap, there are no possibilities to compare this very unique situation of lions hunting cave bears deep in caves during the Late Pleistocene.

4.9. Permanent War with Hyenas. Modern spotted hyenas (the leading female) are normally killed by the leading lion while male lions are rarely killed by hyenas [148]. Late Pleistocene spotted hyenas were feeding at least on dead lions (as similar as their modern relatives) and imported their remains to cave and open air den sites (also similar to modern [94]) which is well documented in the Late Pleistocene of Germany [64, 67] (Table 1). The conflicts are/were about territory, cub protection, and prey [95, 158], but in the Late

Pleistocene, battles in hyena den caves are more frequent, which has only limited modern comparison due to lack of extensive caves present in Africa. The cave “battle model” of the Late Pleistocene predators established for the Zoolithen Cave [45, 46] (Figure 8(b)) demonstrates the cave use by hyenas (entrance area as den) and cave bears (deeper for hibernation). It remains unclear, if both synchronously used cave branches at least at some large cave systems [45]. In the Zoolithen Cave, skull bite trauma pathologies are present at all three animals, hyenas, lions, and cave bears (Figure 8(b)) [68]. Also a misinterpretation was made before here [167] that the damage to cave bear skulls resulted from “Neanderthal hunts” [168] which suggested not to have occurred at all in Europe for the Middle Palaeolithic, but only later with new weapon technology of modern humans in the Aurignacian/Gravettian (projectile fragment in vertebra, cut marks on cave bear bones, projectiles deep in cave bear dens, and pathological cave bear bones with bone projectile damage) [169, 170]. The cranial damage on the Zoolithen Cave lion skull is similar to that which has also been found on other skulls from cave bear dens (Sloup Cave) and hyena dens (Srb-sko Chlum-Komín Cave) in Czech Republic (Figure 7) which are also attributed to battles between lions and cave bears or between lions and hyenas [62, 68]. In all these overlapping hyena/cave bear dens there seems to have been two main “war zones.” The first (zone 1) is at the entrance of a hyena den (battle with hyenas while stealing prey, or killing their cubs), which resulted also in lion kills by hyenas, which is best demonstrated by the ill young lioness skeleton find from the Srb-sko Chlum-Komín Cave hyena prey depot den (Figure 4) [62]. It was proposed that the young lioness with a bite trauma damage, which was possibly excluded from the pride, tried to steal prey from a hyena den prey storage site and was killed by the hyena clan (or it has been imported as complete carcass) [62]. A similar but different site type (scavenging open air site) battle situation was presented for the ill lioness from Neumark-Nord Lake I, which had only one lost upper jaw canine and hind leg trauma illness. There, a scenario is reconstructed where the outnumbered weak lioness was killed because of prey battles with a hyena clan [62]. Most of the cranial trauma damage seems to have resulted by these battles and not from cave bear battles, which also must have happened. Those can be determined by the pathological bones of both top predators (Figure 7). Newly studied traumatic pathologies in lions [68] and hyenas (herein) are different (Figure 7) and are even different from those of the cave bears, which latter abundant and very different types of pathologies must be revised and studied in future with predation and hunting background. As already discussed for lions [68], bite damage causing exostoses bone growth are caused by lions and are found mainly on their skull sagittal crest, the fore, and much less the hind limbs (Figure 7) [68]. Lions struggle with the prey with the forelimbs and attack mainly on the head of the carnivore antagonist [68, 158]. This explains the damage on hyena skulls too, including on their sagittal crest as has been found on at least six skulls (Figure 7). As mentioned in the skull shape types before, healing after strong bite damages causes strong-convex crests such as seen at remains from the Zoolithen Cave and

Brühl-Spieswiesen open air sites. In Late Pleistocene spotted hyenas, other trauma pathologies on the shoulder area are also found in a single example (Srbsko Chlum-Knomín Cave—also possible battle with the afore mentioned lioness) and most often on their distal hind legs (Figure 7). In comparison, modern African spotted hyenas instead attack lions and other hyenas by biting them on the hind legs. The fact that they are much more common on hyenas than lion hind limbs demonstrates that these are results from mainly intraspecies conflicts of hyenas. The war between lions and hyenas is also documented with remains found in larger hyena den bone assemblages (see Table 1) where bones might result either from a kill or only scavenged carcass which hyenas found and imported to the den. Compared to modern African lion and hyenas, their battles result in 50% in each species mortality [148, 171], which must be expected to be similar but with cave bear mortality impact in the Late Pleistocene.

4.10. Late Pleistocene Steppe Lion Cannibalism. In the Late Pleistocene, there was also the war (zone 2 deep in the cave) with the cave bears. These attacks were made mainly on cubs (Figure 7) and from time to time lions must have been killed by the male or females protecting their cubs. These carcasses were not consumed by herbivorous cave bears which explains why lion skeletons in caves are often complete, such as those found in Urşilor Cave (Figure 6). However, one of these subadult lioness skeletons was scavenged by a large top predator (hyena or lion) as suggested by the bite mark sizes. The slight damage on bone joints only and absence of cracked bones might indicate a cannibalistic scavenging by a lion, rather than by a hyena. In this cave area about 800 meters far from the entrance in a second cave level where lions were possibly trapped, and possibly this situation in Urşilor Cave is the only indication for possible lion cannibalism under stress situations, which stress cannibalism was also rarely observed in modern African lions [158]. If this is true, then we have another argument for “lions hunting in packs or pairs” whereas the youngest and weakest one was finally the target of other lions.

5. Conclusions

Late Pleistocene spotted hyena *Crocota crocuta spelaea* (Goldfuss, 1823) and steppe lion *Panthera leo spelaea* (Goldfuss, 1810) are represented in Central Europe by a ratio of 3 hyenas/1 lion remain which is estimated on material from 106 mainly cave and in lesser amount of open air sites. One to three percent of the lion remains at hyena den sites indicate at minimum their scavenging by hyenas, which possibly even killed time by time cubs, adolescents, lionesses, or/and weak individuals, similar as well reported by the African relatives. The extant last hyenas and lions of Europe have similarities in their ecologies to modern African hyenas/lions resulting in competition about prey and territory, whereas only hyenas used caves as den sites. However there are differences to modern African hyenas/lions, because there caves are less abundant, and cave bears (or other bears) are absent, as are

the prey group of cervids. Cannibalism within Late Pleistocene spotted hyenas is documented at many dens, whereas only two individual skeletons from Europe reflect special taphonomic site conditions (vertical-diagonal shafts or prey storage sites). Late Pleistocene spotted hyenas left bone accumulations at three different den types: (1) birth/natal dens, (2) communal dens, and (3) prey storage dens. None of the lion and wolf competitors produced bone accumulations, nor such massive bone damages found within hyena den bone assemblages. Only hyenas developed at all megamammal groups a similar butchering technique, to decompose carcasses, whose body parts (even Neanderthal/Cromagnon human remains of exhumed shallow burials) were imported to dens to avoid conflicts with other predators. Feeding specializations by hyenas, lions, and wolves on different megamammal groups partly overlap (e.g., cave bears). Lions and wolves were specialized cervid (fast running prey) and bovid (large herds) hunters, whereas hyenas were the main meat colossus scavengers and carcass decomposers of woolly mammoth and woolly rhinoceros, which subadults/adults have even for hyenas uncrushable bones. Late Pleistocene spotted hyenas left repeatedly similar damaged large prey bones all over Europe. Similar to modern spotted hyenas, Late Pleistocene ones are expected to have hunted in clans equids (Przewalski horses in the Late Pleistocene-zebras modern). Foetal Przewalski horse remains prove quite uniquely the hunt in spring times at one Czech hyena cave prey storage and communal den site. Steppe lions as open environment (mammoth steppe to boreal forests) felids focused on cervids with reindeer targeting specialization during the Last Glacial Maximum around 22.000 BP., when other megafauna became rarer or extinct. They also must have hunted possibly in packs bovids (steppe bison/aurochs) or saiga antelopes in the steppe or valley environments. Late Pleistocene lions never used caves even for short-term periods; they only dwelled for cave bears, mainly cub hunting. All three top predators (lions, hyenas, and wolves) fed (hunted or scavenged) on cave bears in boreal forest of middle high elevated (150–650 a.s.l.) mountain regions (lions even up to elevations of 1,500 a.s.l.) which caused deathly conflicts in caves between all of them (inter-/intraspecies fights) that have no modern analogue. Those battles caused bite damages especially on their skulls and legs, which produced different postcranial, but similar cranial bite damage pathologies. Some of the bite marks also found at lion skeletons and bones cannot be separated clearly in their alive or postmortal origin.

Conflict of Interests

The author declares that there is no conflict of interests regarding the publication of this paper.

Acknowledgments

The author thanks all the museums and institutions mentioned and their curators for their support to study bone material from various sites in Germany, Czech Republic, Austria, and England. The company and private research

institute Paleologic (www.paleologic.eu) sponsored the science to the “European Ice Age Spotted Hyena Project.” A first critical review and spell check was made thankfully by Dr. G. Zazula from the Beringeria Center, Canada. Dr. M. Sabol also commented on a first draft. J. McNamara (World Museum of Man, www.worldmuseumofman.org) supported the paper with photos of the Austrian Badel Cave lion and hyena skulls and made a paper spell check. Finally G. Teichmann contributed the hyena, lion, and cave bear illustrations.

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