

Thick skin cutters of Siberian frozen mummies—The coevolutionary adaptation of Eurasian Ice Age spotted hyenas

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Abstract

Siberian extinct top predators—Ice Age spotted hyenas—are discovered in the permafrost of Yakutia in-between frozen mammoth, rhinoceros, bison or horse carcasses, such as in Mongolia at new open-air sites. Historic described European holotypes and new crania from Siberia, Mongolia, and Europe allow presenting the monophyly of *Crocota* reaching back 2.53 Mio years (Late Pliocene). Spotted hyenas coevolved in dental change and body size to their largest guilt, thick-skinned elephants and rhinoceroses. The Late Pleistocene (MIS 5d-3, 113.00–25.000 BP) *Crocota crocuta spelaea* (Goldfuss, 1823) is proven to have scavenged Siberian woolly rhinoceros *Coeleodonta antiquitatis* (Blumenbach, 1799) carcasses. Rhino mummy skins have scavenging signs attributable only to hyenas. Chew cuts of breaking-cutting scissor dentition are found at mummy skins. The last Eurasian hyenas left always similar chew-damaged woolly rhinoceroses' crania with braincase openings and damaged mandibles, whereas their deep bite scratches are often found on the distal joints of long bones. Strongest rhino bone damage is found at natal den sites (cave or open air), to which hyenas imported guilt to their cubs. The recently known Ice Age spotted hyena palaeobiogeography overlaps exactly with those of woolly rhinoceros and mammoths. All reached Bering Straits.

KEYWORDS

dental evolution, East Siberian palaeobiogeographic extension, Eurasian revision, phylostratigraphy, Pleistocene spotted hyenas, Siberia, Siberian frozen mummies, woolly rhinoceros scavenger

1 | INTRODUCTION

The “IceAgeSafari landscape” of Siberia is a thermokarstified permafrost in north-eastern Russia (Figure 1a) (Anisimov & Nelson, 1996; Séjourné et al., 2015). The region of Yakutia became very famous since 1799 by the frozen Adam's mammoth discovery, Ice Age megafauna skeletons, large amounts of well-preserved bones (Figure 1b) and its traded mammoth ivory (Popatova et al., 2018). Most spectacular are icy carcasses (frozen mummies) or partly complete skeletons of extinct Ice Age animals that have been discovered mainly along with the Siberian arctic coast or river terrace melting

ice (Lazarev, 2008; Popatova et al., 2018) (Figure 1b). This potential UNESCO natural world heritage region and its extinct mammoth steppe megafauna are one newer research focus internationally with rising amounts of discoveries of frozen mammoths, rhinos, bison, horses and rare predators (Brandt, 1849; Brandt, 1849; Lucas, 1898; Tolmachoff, 1929; Tolmachoff, 1929; Russanov, 1968; Skinner & Kaisen, 1974; Sokolov, 1982; Sokolov, 1982; Novikov, 1993; Aplan & Harington, 1994; Nagaoka et al., 1996; Mol et al., 2001; Maschenko et al., 2005; Maschenko et al., 2005; Maschenko et al., 2006; Boeskorov et al., 2007; Lazarev, 2008; Vasiliev, 2008; Eisenmann & Sergej, 2010; Kirillova et al., 2011; Boeskorov et al., 2011; Kirillova et al., 2012; Fisher

et al., 2012; Spasskaya et al., 2012; Maschenko et al., 2012; Boeskorov et al., 2013; Maschenko & Boeskorov, 2013; Fisher, 2014; Kirillova, Zanina, et al., 2015; Kirillova, Tiunov, et al., 2015; Maschenko et al., 2015; Baryshnikov, 2015; Popatova et al., 2018) (Figure 1c). The mammoth tusk hunters and other bone collecting activities recently uncover other rare and also smaller finds.

The first top predator, the Siberian lion *Panthera leo vereshchagini* Baryshnikov & Boeskorov, 2001, was described from there by crania and isolated bone finds (Vereshchagin, 1971; Baryshnikov & Boeskorov, 2001), such as a newer first skeleton discovery of 2008 (Kirillova, Zanina, et al., 2015; Kirillova, Tiunov, et al., 2015). Most recently, in 2015, it is also known by two frozen cubs (Protopopov et al., 2016). The second top predator and the most impacting big game carcass scavenger, the Ice Age spotted hyena *Crocota crocuta spelaea* (Goldfuss, 1823) (Goldfuss, 1823; Diedrich, 2008, 2010a,b, 2011a,b), was unknown from West to East Siberia thus far. This most important taphonomic carnivore agent, the specialized thick skin cutter, heavy carcass decomposer and strongest bone damager of the world (Diedrich, 2012a,b, 2013a,b) has not become yet into the focus of discussion to any Siberian frozen mammoth or rhinoceroses' carcasses. Some large carnivore bites have been even misidentified as "ground squirrel bites" on bison carcass bones (cf. Shpansky et al., 2016), although signs of "large carnivores" have been mentioned before for other carcasses without further discussion (cf. Boeskorov et al., 2007; Boeskorov et al., 2011).

Recently, the few hyena carnivore bones have been sold all on the private fossil market, especially over the e-bay platform which new Siberian-Mongolian Late Pleistocene spotted hyenas material builds one base for this study. After information, a large Russian collection went this year to Hong Kong (China) including over a hundred woolly rhinoceros skulls, and all the herein published four hyena crania and 12 mandibles, which are now distributed throughout the globe. In order not to lose this information, although the material is in private collections, it is highly relevant to document at this information through this work. The author helped to save at least two crania and some mandibles for scientific purposes, which are possible to figure in anatomic standards and with some main important data. The other material was taken from the available photographs of the internet seller platforms. The other material which was used for the taxonomic preliminary revision of the Pleistocene spotted hyenas is instead kept in various museums or university collections.

The extinct Ice Age spotted hyena fossil record is extended herein by the new cranial remains from several Middle-Eastern Siberian Russian and adjacent Mongolian highland finds (Figure 1d). Those are clearly selective and postcranial material must be present but was not collected or yet identified as such. The open-air site collected cranial remains (crania and lower jaws) are the key for (a) hyena scavenging

site (Figure 1d) or. (b) first open-air natal den site identifications in the permafrost landscape close to the Bering Bridge mapping the indirect proof for former hyena presence where their bone record is absent in non-cave lowland regions and is based on the chew and bite damages at guilt carcass skins and bones (cf. Turner et al., 2001; Turner, 2010). Those direct and indirect records extend their Eurasian phylostratigraphy and palaeobiogeography such as knowledge about natal dens in the open landscape.

To understand the new Siberian and Mongolian material (Figures 2–4) and its relationship to the European and Asian described material, a first review of the southern Russian Ural, Altai Mountain and Far East Russian coast cave sites (cf. Baryshnikov & Vereshchagin, 1996; Baryshnikov, 2014; Kosintsev, et al., 2015; Kalmykov & Kobylkin, 2017) is presented in a new paleobiogeographic map (Figure 5).

Another review is presented preliminary on the fossil holotype crania record compilation which was made herein for the first time, based on many forgotten museum specimens. The European and Asian Pleistocene spotted hyena records are revised herein only, although all three valid genera (*Crocota*, *Parahyaena*, and *Hyaena*) with their monophyletic lines were studied parallel (publication elsewhere), covering their final fossil record for the past 2.53 Mio years. The cranium, lower jaw, and especially dental morphology comparison, include all historic holotypes and other relevant originals (cf. Figure 5). Most of those forgotten European type specimens have not been compared in any of the former papers to the Asian records. The latter therefore has been described always later under new names or combined two different genera mandibles and crania. Into this overview revision, the new East Siberian, Mongolian and Inner Mongolian Chinese discoveries and new undescribed European crania from various hyena den sites and different periods allow presenting a monophyletic *Crocota* lineage reaching back at least 2.3 Mio years ago and perhaps even further. Furthermore, other fossil hyenas, belonging to subspecies of the extant African brown hyena *Parahyaena brunnea* and striped hyena *Hyaena hyaena*, are initially revised in the Pleistocene Eurasian record. This is very important to understand past misidentifications on the genus and species levels. Only three Pleistocene hyenas *Crocota*, *Parahyaena* and *Hyaena* roamed Europe competitive for the past 1.3 Mio years extending further north during warm periods or interglacials. Only one of them finally survived longer in Eurasia after the Holsteinian Interglacial about 280.000 BP, the specialized and climatic more independent adapted and cave-dwelling spotted hyena (Figure 5).

Taphonomic comparisons to African spotted hyenas and their thick-skinned elephant and rhinoceros guilt butchering allow a more complete understanding of Siberian frozen mummy carcass skin and bone damages (Figure 6). Skin damage on an initially scavenged Zambian African

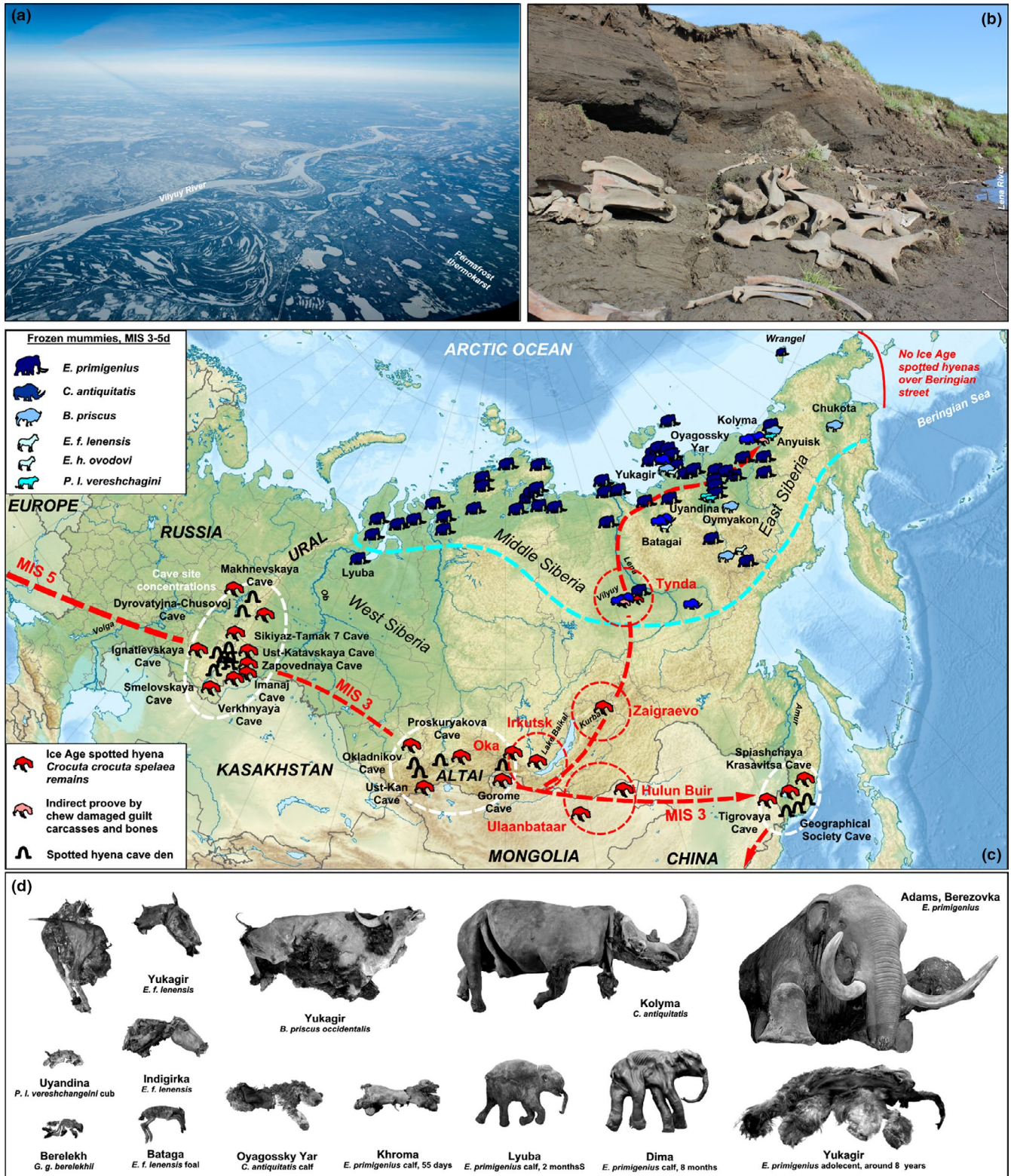


FIGURE 1 (a) Vilyuy River thermokarst permafrost landscape. (b) Mammoth bones at the Lena River terrace margins, from <http://beta.mammothportal.com/?page=2>. (c) Reported and new Ice Age spotted hyena cranium and mandible sites of eastern Siberia (Tynda, Irkutsk, Zaigraevo) and Mongolia (HulunBuir, Ulaanbaatar). (d) Compiled frozen mummies of the famous Adams mammoth and newer discoveries. Modified and partly mirrored mummy photographs compiled from: Tolmachoff (1929), Russanov (1968), Sokolov, (1982), Apland and Harington (1994), Mol et al. (2001), Maschenko et al. (2005), Maschenko et al. (2006), Boeskorov et al. (2007), Vasiliev (2008), Lazarev (2008), Eisenmann and Sergej (2010), Boeskorov et al. (2011), Kirillova et al. (2011), Kirillova et al. (2012), Kirillova, Zanina, et al. (2015)); Kirillova, Tiunov, et al. (2015)), Fisher et al. (2012), Spasskaya et al. (2012), Maschenko et al. (2012), Boeskorov et al. (2013), Maschenko and Boeskorov (2013), Fisher (2014), Shpansky et al. (2016); Protopopov et al. (2016), Popatova et al. (2018). Extinct Ice Age spotted hyena *Crocota crocuta spelaea* (Goldfuss, 1823) sites compiled from Baryshnikov and Vereshchagin (1996), Baryshnikov (2014), Kosintsev et al. (2015), Kalmyko and Kobylkin (2017) with new site regions

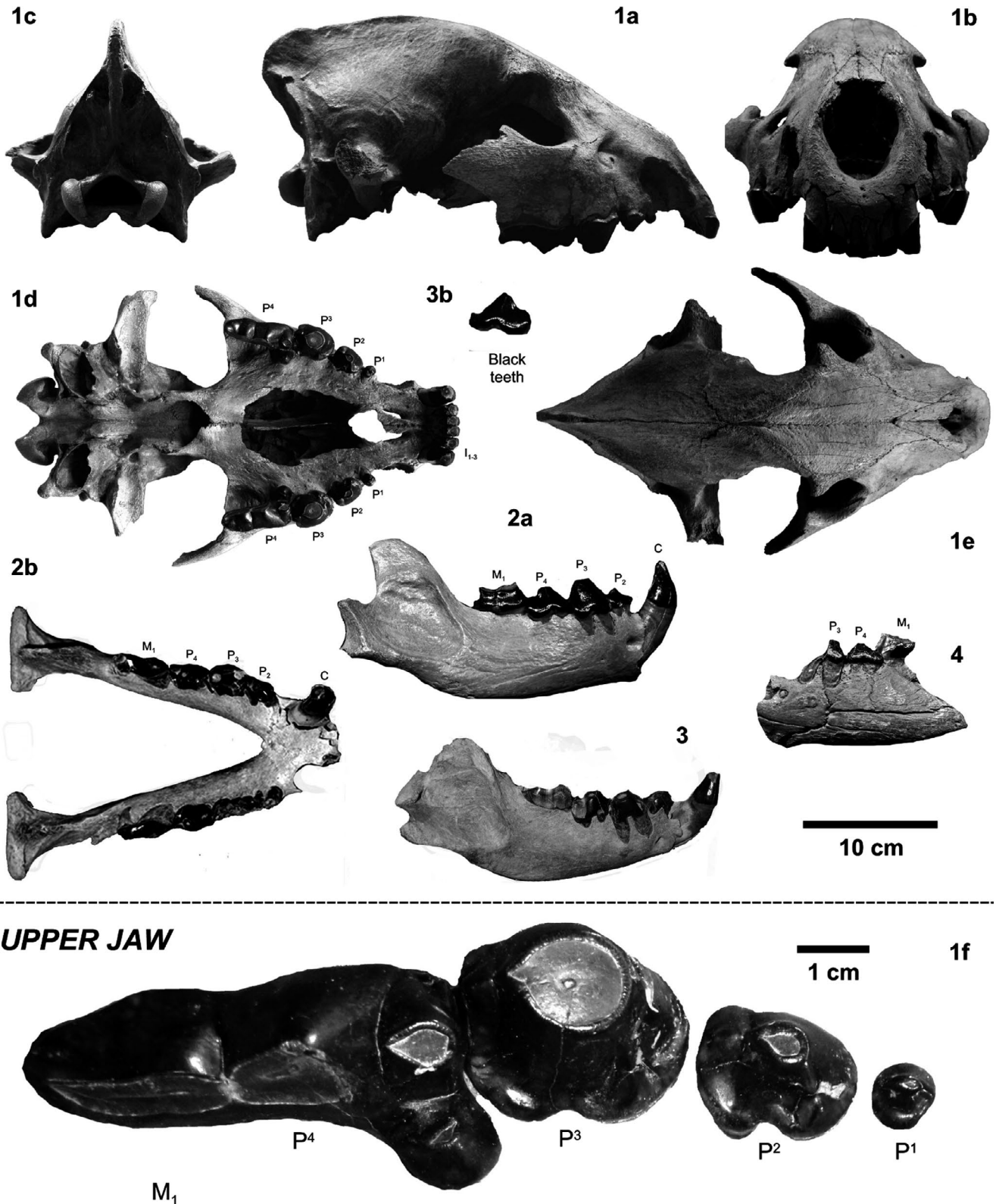


FIGURE 2 Extinct Late Pleistocene Ice Age spotted hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) cranial remains from Hulun Buir region, Inner Mongolia, China. 1. Cranium (coll. HH), a. Lateral, b. Cranial, c. Caudal, d. Ventral, e. Dorsal, f. dental details enlarged. 2. Lower jaw of adult (former coll. NIN), lateral and dorsal. 3. Lower jaw of older adult (former coll. HEN), lateral. 4. Left mandible fragment (former coll. HEN), nearly lateral. (Photographs 1. Hartnagel, 2–4: Internet sources: <https://ninijian.com/> and www.henskensfossils.nl/)

elephant was photographed (White & Diedrich, 2012) for comparisons on Ice Age mummy skin damages. Newer film sequences (Films 7 and 8) of hyenas scavenging and

decomposing African elephant and rhinoceros carcasses support a complete understanding of the similar feeding strategies of the past.

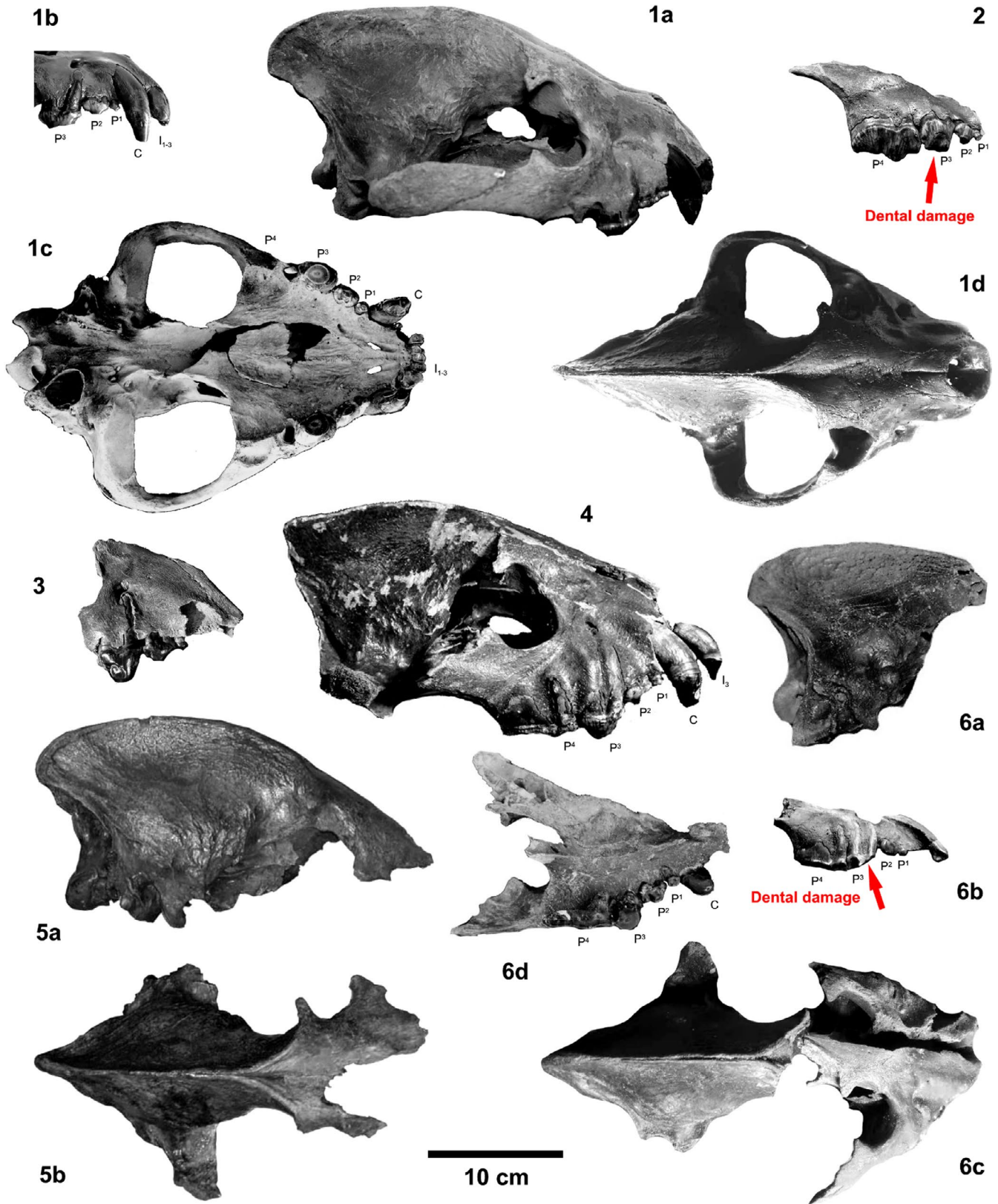
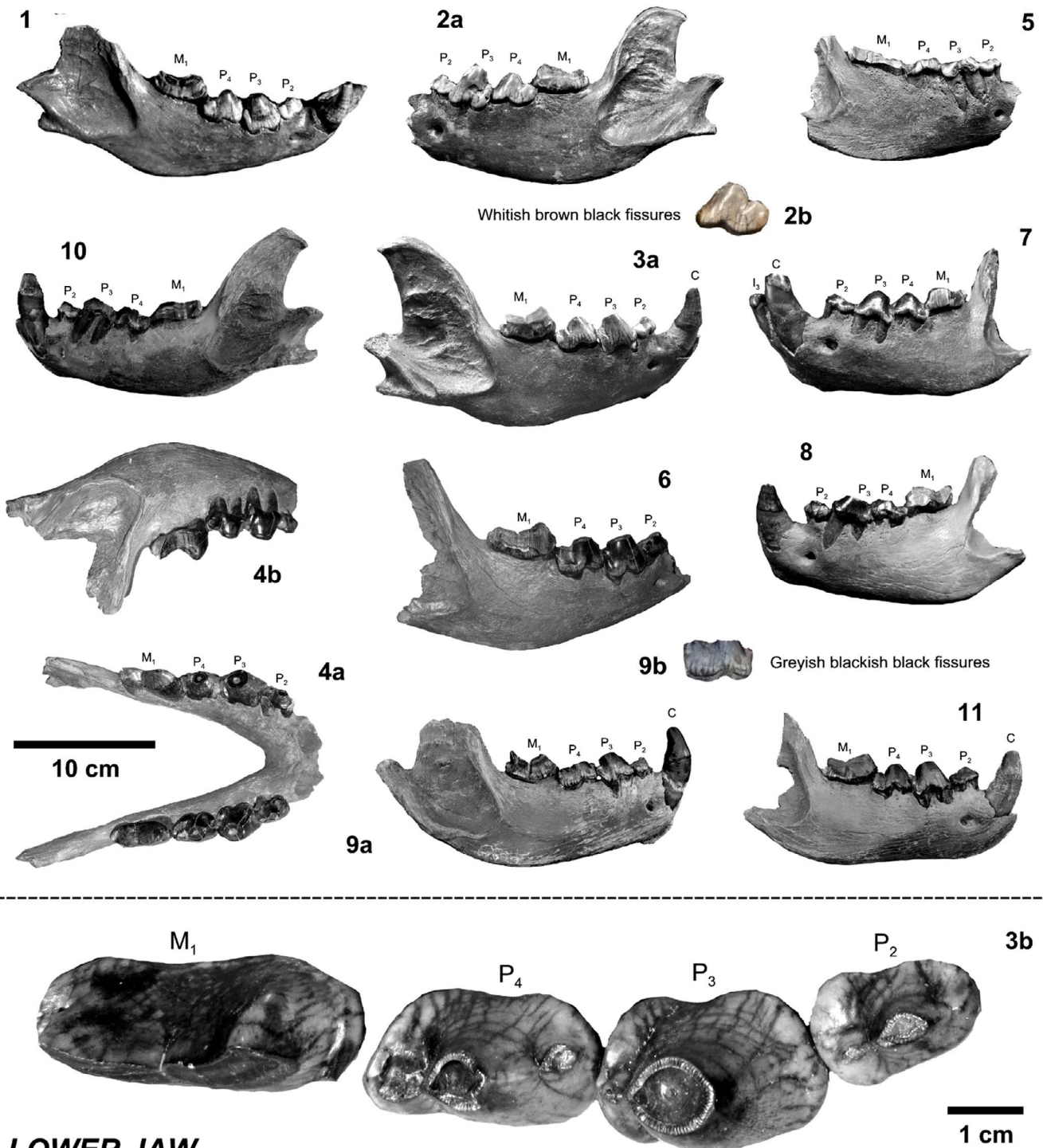


FIGURE 3 Extinct Late Pleistocene Ice Age spotted hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) cranial remains from along the Vilyuy River of the Tynda region, North-East Siberia, and Irkutsk region, South-East Siberia, Russia. 1. Cranium of older adult from Irkutsk region (coll. ME). A. Lateral, b. Lateral detail, c. Ventral, d. Dorsal. 2. Maxillary of early adult from Tynda region (former coll. HEN), lateral. 3. Right maxillary from Irkutsk region (former coll. HEN), lateral. 4. Skull from Tynda region (former coll. HEN), lateral. 5. Skull from Zaigraevo, along Kurba River in Buryat Republic, Russia (coll. CCMGE 2–3922), a. Lateral and b. Dorsal. 6. Skull from Ulaanbaatar, Mongolia (former coll. <https://ninijian.com/>), a. Brain case lateral, b. Maxillary left lateral, c. Dorsal, d. Maxillary right ventral (Photographs Internet sources: <https://ninijian.com/> and www.henskensfossils.nl/)



LOWER JAW

FIGURE 4 Extinct Late Pleistocene Ice Age spotted hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) lower jaw remains from along the Vilyuy River of the Tynda region, North-East Siberia, and Irkutsk region, South-East Siberia, Russia. 1. Lower jaw of older adult from the Tynda region (former coll. HEN), lateral. 2. Right mandible from the Tynda region permafrost (former coll. HEN), a. Lateral, b. Typical white brownish tooth colour preservation in the permafrost. 3. Mandible of late adult from Irkutsk region (coll. HH), a. Lateral left, b. Dorsal, c. Lateral right, d. Occlusal dental details enlarged. 4. Lower jaw from the Tynda region, Siberia, Russia (coll. HH Croc-3), a. Dorsal, b. Ventral. 5. Lower jaw from the Tynda region (former coll. HEN), lateral. 6. Lower jaw from the Tynda region (former coll. HEN), lateral. 7. Lower jaw from the Tynda region (former coll. HEN), lateral. 8. Lower jaw from the Tynda region (former coll. HEN), lateral. 9. Left mandible (mirrored) from Irkutsk region (former coll. HEN), a. Lateral, b. Greyish-blackish tooth colour. 10–11. Mandibles of old animals, from Siberia, without exact localities (Photographs Internet sources: <https://ninijian.com/> and www.henskensfossils.nl/)

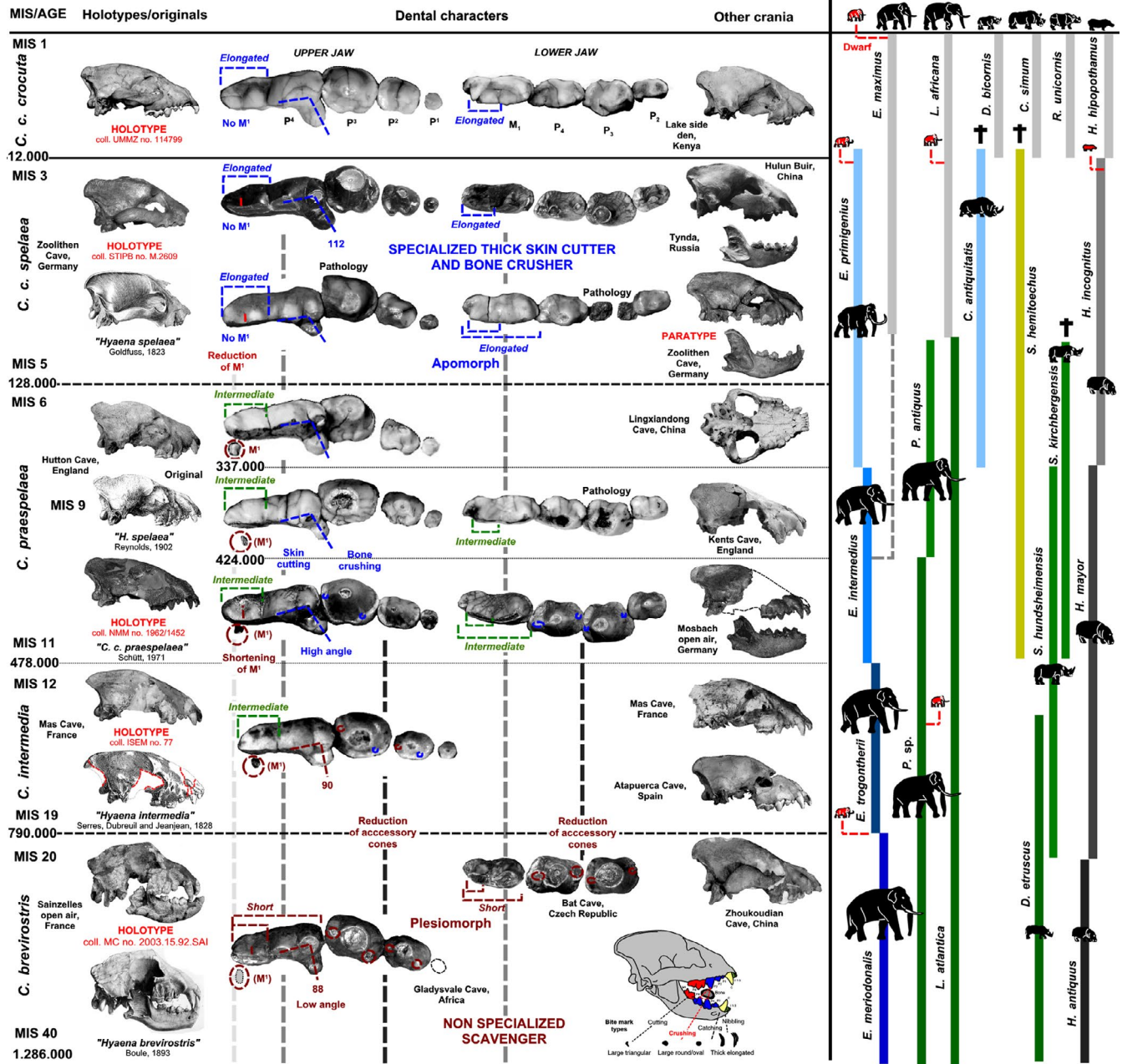


FIGURE 5 Dental comparison of extinct Early to Late Pleistocene monophyletic line of Eurasian spotted hyena *Crocuta* in comparison to extant in Africa. The breaking scissor dentition of the upper and lower jaw modified from unspecialized scavenger to specialized perfect thick skin cutter and bone crusher function by reducing premolar cusps, elongating the P⁴ and M₁ and loss of the small M¹. Crania, mandibles and dentition material see details and collection abbreviations in material and methods. Holotype crania illustrations from the historic publications of Goldfuss (1828); Boule, 1893; Serres et al. (1828), one cranium from Reynolds (1902). Chronostratigraphy, MIS stages and absolute data according to Lisiecki and Raymo (2005). Several crania or mandible dentitions are mirrored

2 | FROZEN BIG GAME MUMMIES AND LARGE CARNIVORE FEEDING SIGNS

Northern Middle and East Siberia plains have large-scale ground ice along the Arctic coasts of the west to east Siberia and the New Siberian Islands which natives called "Edoma" (Nagaoka et al., 1996). The Edoma Formation

contains multiple ice lenses and several peat layers. It is also thermokarstified by sinkholes and is cut by Vilyuy, Lena or Kolyma braided rivers. Along these river areas especially, carcasses and bones appear every year (Figure 1a,b). The Edoma Fm is mainly composed of massive ground ice with pillar-shaped frozen soil (Nagaoka et al., 1996). The lower part below the ice ranges in absolute radiocarbon ages 59.000 years and falls into the early Late Pleistocene

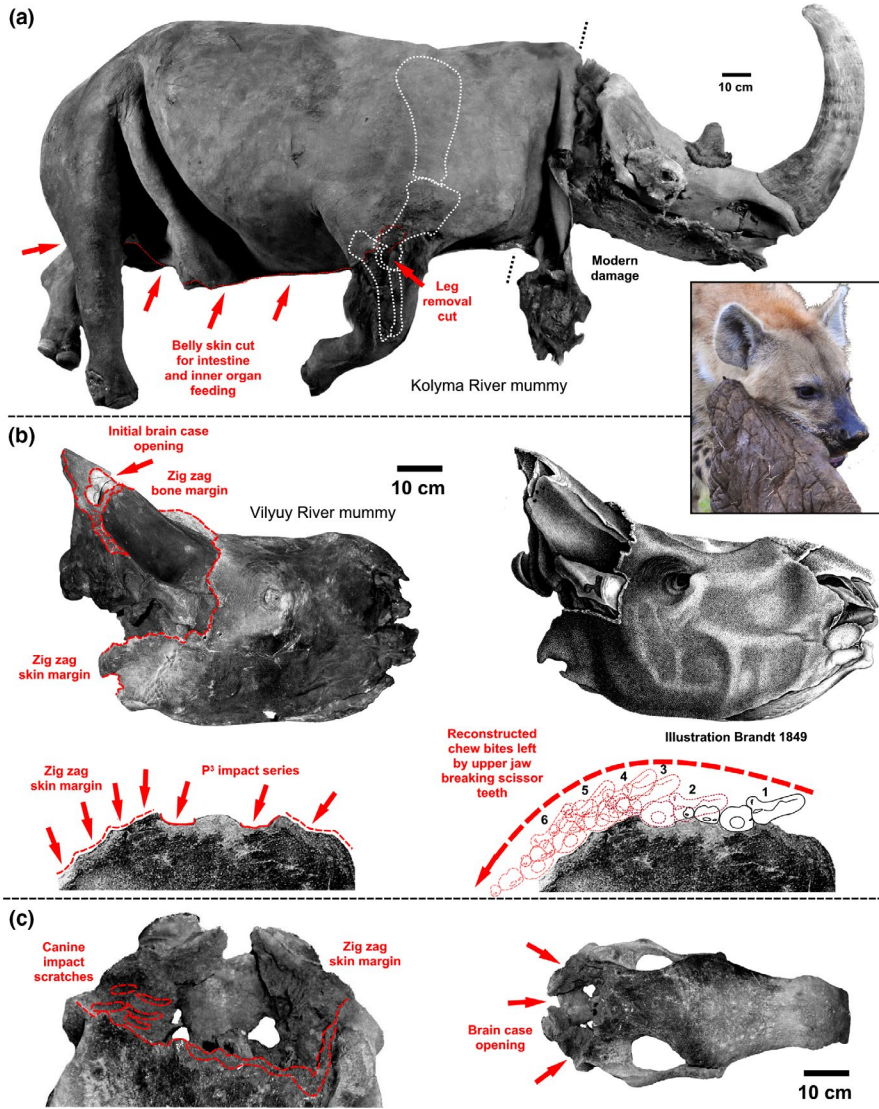


FIGURE 6 Ice Age spotted hyena chew-cut damaged woolly rhinoceros *Coelodonta antiquitatis* thick skins and comparison to African thick skin cut made by a modern spotted hyena. A. Nearly complete carcass but without intestines and inner organs of the mummified bull from Kolyma River estuary found in 2011 (photograph modified from Popatova et al., 2018). B. Head of the partly preserved mummy from the Vilyuy River discovered in 1771 (photograph from Popatova et al., 2018, illustration from Brandt, 1849). C. Subadult cranium with typical hyena brain case opening from unknown Siberian site (spotted hyena photograph modified from Shutterstock)



FILM 7 Hyena sticks head in elephant's butt, eating giants: Elephant. <https://www.youtube.com/watch?v=OX9xCo183VA>.



FILM 8 Hyenas devouring a rhino carcass. <https://www.youtube.com/watch?v=ioGqXAbPxxo>.

Marine Isotope Stage (MIS) 5–4. The middle part of the frozen Formation is dated between 40.000–24.000 BP into the MIS 3. Most of the frozen carcasses are from the Late Pleistocene 59.000–24.000 BP of the MIS 4–3 and older

MIS 5 (Tolmachoff, 1929; Sokolov, 1982; Novikov, 1993; Mol et al., 2001; Maschenko et al., 2005; Maschenko et al., 2006; Boeskorov et al., 2007; Lazarev, 2008;

Boeskorov et al., 2011; Kirillova et al., 2011; Kirillova et al., 2012; Fisher et al., 2012; Spasskaya et al., 2012; Boeskorov et al., 2013; Fisher, 2014; Maschenko et al., 2015; Shpansky et al., 2016; Popatova et al., 2018). From the upper permafrost with peat lenses (11.000–7.000 BP, MIS 2–1 (Nagaoka et al., 1996)) Early Holocene megafauna mummies are known by moose (Lazarev, 2008) or wolverine (Baryshnikov, 2015). Since 1799, frozen mega mammal carcasses have been discovered in Siberia (Popatova et al., 2018). A new wave of mummy discoveries started in 2001 with the Jarkov mammoth discovery by Mol et al., (2001) with the latest finds being reported in 2017 (Maschenko et al., 2017). All newer and relevant older mummies are reviewed herein for an initial discussion about possible carnivore impacts.

2.1 | Woolly mammoth

With the first discoveries of an incomplete *Elephas primigenius* Blumenbach 1799 frozen carcasses by Adams in 1799 (cf. Figure 1d), Berezovka in 1901, or Sanga-Yuryakh in 1908, further frozen partly preserved mammoth individual discoveries have been reported in the past. The newer calf and adolescent mummies have been described between 1972 and 2018 from Lyakhov, Berelekh, Shandrin, Maksunuokha and Yukagir (cf. Figure 1d), from Dima Creek, Magadan District, Masha, Yamal Peninsula, Abyi, Luba, Oymyakon or Khroma (Tolmachoff, 1929; Sokolov, 1982; Mol et al., 2001; Maschenko et al., 2005; Maschenko et al., 2006; Boeskorov et al., 2007; Lazarev, 2008; Boeskorov et al., 2011; Kirillova et al., 2011; Kirillova et al., 2012; Fisher et al., 2012; Spasskaya et al., 2012; Boeskorov et al., 2013; Fisher, 2014; Maschenko et al., 2015; Popatova et al., 2018). Examination of those mummies has improved the anatomic knowledge about soft tissues, inner organs or intestines, ear, trunk and foot morphology details, such as hair colour or complete DNA knowledge, but also their food choice. Any study focusing on their predation or carcass scavenging by top predators Siberian lions or Ice Age spotted hyenas or wolves as yet has not been conducted. Some figured mammoth skins seem to have been cut either by lions or hyenas, but all available photographs in publications are not good enough to identify secure scavenging signs. Also, the guilt bones are generally figured to be selected with the complete or have been damaged by excavations.

2.2 | Woolly rhinoceroses

The woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799) discovery of the Vilyuy River (Eastern Siberia) of 1771 was described in 1849 (Brandt, 1849). It becomes now the

key specimen to identify its only or main scavenger, which is indeed spotted hyenas. This and another woolly rhinoceroses' carcass have overlooked thick skin chew-cut damages, which only top predators might have produced with their breaking scissor dentition. The second important key specimen, the Kolyma woolly rhinoceros (cf. Boeskorov et al., 2011). (cf. Figure 1c), is herein discussed in the context of hyena guilt butchering strategies. It was only mentioned in its first description to have an open belly such as missing most of the intestines and inner organs (cf. Boeskorov et al., 2011). The Oyagosski Yar woolly rhinoceros is one of the newer and first calf discoveries, which has no signs of large carnivore damage (Boeskorov et al., 2013).

2.3 | Horses and donkeys

The small caballoid horse *Equus ferus lenensis* (Russanov, 1968) (cf. Figure 1d) cranium from the Lena River delta was described in 1968 (Russanov, 1968). This horse seems to be represented furthermore by new incomplete frozen horse mummies, which is not osteometric or DNA confirmed. The identification of the smaller stenoid donkey *Equus hemionus ovodovi* (Russanov, 1968) is based also on cranial remains, but from an Ice Age spotted hyena den cave bone assemblage in the Ural (Eisenmann & Sergej, 2010). The Ice Age donkey seems to be represented also in the “horse mummy” record, which is not yet identified at the newer Selerikan, Dyukarski, Yukagir and Batagai foal horse or possible donkey finds (Lazarev, 2008; Spasskaya et al., 2012; Boeskorov et al., 2013). The Yukagir horse skin was punctured not only with round-oval holes but also claw scratches comparable to claw-sizes of “large predators” (cf. Boeskorov et al., 2013). This would indicate a lion rather than a hyena kill, because of both top predators only lions catch their prey with their sharp claws (e.g. White & Diedrich, 2012). Such claw scratches are similarly known at the frozen steppe bison carcass of Alaska, called “Blue Babe” (Guthrie, 1990). The upper part of the horse snout including the frontal maxilla is missing and was probably eaten along with the front legs and the rest of the torso (cf. Figure 1c) (cf. Boeskorov et al., 2013).

2.4 | Bison types

Two different bison species have been distinguished for the Siberian Pleistocene-Holocene record. One is the larger Eurasian Late Pleistocene steppe bison *Bison priscus* Bojanus, 1827 with its short-wide metapods (cf. Figure 1d). The other smaller North American-Siberian Holocene bison *Bison bison occidentalis* (Lucas, 1898) has longer metapods and smaller horns (cf. Lucas, 1898; Skinner & Kaisen, 1974;

Guthrie, 1990; Apland & Harington, 1994; Vasiliev, 2008; Shpansky et al., 2016). The Mylakhchin, Yana, Tsiigehtchic and newest Holocene bison mummies from the Rauchua River (Lazarev, 2008; Boeskorov et al., 2013; Kirillova, Zanina, et al., 2015; Kirillova, Tiunov, et al., 2015) include no reports about carnivore impact, nor allow photographs identifying such. Instead, the Late Pleistocene (MIS 3, 44.618–49.824 BP) steppe bison skeleton from Krasniy Yar proves its scavenging and dismembering by large carnivores, which left only some body parts at the scavenging site. Possibly, those body parts represent already carnivore deported body pieces, which might be in some cases in hyena open-air prey depot context. Large carnivore canine bite scratches in the spongiosa of the ventral side of the C6 and 7 vertebrae of an articulated column were misidentified as rodent bites (Shpansky et al., 2016). Those are about 4–6 mm wide and deep bite impacts are more suitable in sizes fitting to a hyena or lion canines and incisors which leave around 6 mm wide elongated grooves (Diedrich, 2008, 2012a, 2013b). Their width depends on the depth or bite angle and is therefore highly variable (Diedrich, 2013b). Furthermore, all dorsal cervical spines of the bison column have been chew-cracked off by strong breaking scissor teeth. Hyenas are also the most potential scavengers in this case. The bite scratch position below the column is typical of the carcass consuming strategy in which the predator starts out by eating from the inside the body cavity, consuming first the intestines and inner organs. Although all three large predators, extinct lions, hyenas and wolves practised this in the Ice Age and still extant species use this practice (White & Diedrich, 2012; Diedrich, 2013b), only hyenas or rarer lions leave in most cases such strong bite damage on the columns (Diedrich, 2013b).

2.5 | Siberian lions

Siberian lions became known first in their single crania and bone record (Vereshchagin, 1971; Baryshnikov & Boeskorov, 2001). They have been and are still incorrectly named “cave lions” such as in the first MIS 5–3 aged Late Pleistocene skeleton discovery from Anyuisk in 2008 (Kirillova, Zanina, et al., 2015; Kirillova, Tiunov, et al., 2015). The “cave lion” is indeed a different European subspecies with *P. l. spelaea* Goldfuss, 1823 which was revised to represent no cave animal being already renamed to European Ice Age “Steppe lion” (Diedrich, 2008, 2014). All Siberian material must belong to the “Siberian lion” *Panthera leo vereshchagini* Baryshnikov & Boeskorov, 2001 (Baryshnikov & Boeskorov, 2001) taking the DNA analyses (e.g. Diedrich, 2014) into account, that separates the Siberian lion palaeobiogeography most far west with the Ural Mountain chain boundary (e.g. Barnett et al., 2009;

Diedrich, 2014). The first two mummified Siberian lion *P. l. vereshchagini* cubs (cf. Figure 1d) were discovered in 2015 close to each other on the banks of the Uyandina River (Protopopov et al., 2016).

2.6 | Ice age spotted hyenas

From West to East Siberia, mummies of the second top predator, the Ice Age spotted hyena *Crocota crocuta spelaea* (Goldfuss, 1823), are unknown. For long, the question remained unsolved; whether the second top predator and main scavenger of the woolly mammoth and woolly rhinoceros retreated or remained together with its main large guilt in Siberia before their final extinction in Europe around 24.000 BP (Rohland et al., 2005; Diedrich, 2014). First reports of their presence are known for some caves in Russia: the Ural, Altai and the Far East including the Geographical Society Cave (Baryshnikov & Vereshchagin, 1996; Turner et al., 2001; Turner, 2010; Baryshnikov, 2014) (cf. Figure 1c, Table 1).

2.7 | Wolverines

The Berelekh wolverine “*Gulo gulo berelekhii* Novikov, 1993” mummy (Baryshnikov, 2015) (cf. Figure 1d) was believed to belong to an extinct Holocene Holarctic Eurasian small subspecies. It is a younger synonym to the extant Holocene Siberian *G. g. jacutensis* Novikov, 1993 (Novikov, 1993). This is indeed much different in its posterior tooth morphology and generally larger size to the European Late Pleistocene *G. g. spelaeus* (Goldfuss, 1818) (Diedrich, 2019), which is also known from the Far East Geographical Society Cave (Baryshnikov, 2015).

3 | MATERIAL AND METHODS

Modern extant African hyena skulls are used from the University of Michigan Museum of Zoology, which is all available online with photographs of different views in the database. Herein chosen are the three holotype type specimens in the osteological record to each species: 1. Brown hyena *Parahyaena brunnea brunnea*, cranium with mandible, adult, coll. UMM no. 95748, https://animaldiversity.org/accounts/Parahyaena_brunnea/specimens/, 2. Striped hyena *Hyaena hyaena hyaena*, cranium with mandible, adult, coll. UMM no. 168360, https://animaldiversity.org/accounts/Hyaena_hyaena/specimens/, 3. Spotted hyena *Crocota crocuta crocuta*, cranium with mandible, early adult, coll. UMM no. 114799, (https://animaldiversity.org/accounts/Crocota_crocota/specimens/).

TABLE 1 Russian Ice Age spotted hyena den and scavenging sites (see Figure 1c), absolute data compiled from (Baryshnikov & Vereshchagin, 1996; Baryshnikov, 2014; Kosintsev et al., 2015; Kalmyko & Kobylkin, 2017) and preliminary den type identifications

Makhnevskaya Cave, Ural	MIS 3:37.700 ± 360	Natal and communal den
Dyrovatyjna-Chusovoj Cave, Ural		Communal, prey depot den
Ignatievskaya Cave, Ural	MIS 5–3: >62.300, 47.500 ± 900, >40.100, MIS 3:40.240 ± 380, 44.300 ± 600	Communal, prey depot den
Smelovskaya Cave, Ural	MIS 5–4: >60.800, >59.80 MIS 3:46.200 ± 1,500	Communal, prey depot den
Sikiyaz-Tamak 7 Cave, Ural	MIS 3: >47.600	Communal, prey depot den
Ust-Katavskaya Cave, Ural	MIS 5–4: >59.200 MIS 3:35.650 ± 450	Communal, prey depot den
Zapovednaya Cave, Ural	MIS 5–3	Communal, prey depot den
ImanajCave, Ural	MIS 5–3	Communal, prey depot den
Verkhnyaya Cave, Ural	MIS 5–3	Communal, prey depot den
Okladnikov Cave, Altai	MIS 5–3	Communal, prey depot den
Ust-Kan Cave, Altai	MIS 5–3	Communal, prey depot den
Proskuryakova Cave, Altai	MIS 5–3	Communal, prey depot den
Gorome Cave, Altai	MIS 3:26.180 ± 810, 30.940 ± 700	Communal den
Irkutsk, Oblast River, South-Middle Siberia	MIS 5–3	Open-air site
Zaigraevo, Kurba River, Middle Siberia	MIS 5–3	Open-air site
Tynda, Vilyuy River, Middle Siberia	MIS 5–3	Open-air den site
Spiashchaya Krasavitsa Cave, Far East Russia	MIS 5–3	Communal, prey depot den
Tigrovaya Cave, Far East Russia	MIS 5–3	Communal, prey depot den
Geographical Society Cave, Far East Russia	MIS 5–3	Natal den
Vyluy River <i>C. antiquitatis</i> , Middle Siberia	MIS 3	Open-air scavenging site
Kolyma River <i>C. antiquitatis</i> , East Siberia	MIS 3:39,140 ± 390	Open-air scavenging site

3.1 | Institutional abbreviations

Historic Pleistocene fossil collected holotype type skulls or crania have been studied on the originals in the following collections: “*Hyaena brevirostris*” Boule, 1893 skull, Musée Crozatier, Le Puy-en-Velay, France (=MC, no. 2003.15.92.SAI). “*Hyaena intermedia*” Serres et al., 1828, Institut des Sciences de l'Evolution de Montpellier, France (=ISEM). Mosbach open-air site material with first time figured complete type specimen of “*Crocota crocuta praespelaea* Schütt, 1971,” Naturkundemuseum Mainz (=NMM, 1962/1452). Type cranium to “*Hyaena spelaea* Goldfuss, 1823” from the German Zoolithen Cave, Steinmann Institute Bonn, Germany (=STIPB, no.M.2609).

Other new comparative fossils Pleistocene material is presented herein from the Bat Cave in Bohemia, the Czech Republic, which is kept by the EU registered PaleoLogic Private Research Institute (=PAL). The English Hutton Cave cranium original of Reynolds (1902) was photographed in the Somerset Museum (=SSM), the Torquay Cave cranium is in the Oxford University Museum (=OUM). Torbryan Cave or Banwell Cave material that was also studied is kept in the English Museum of Natural History London (=BMNHL)

and the Natural History Museum of the Humboldt University Berlin (=MB). The Zhoukoudian Cave cranium from China is preserved in the Orlov Museum Moscow (=OMM).

New late Pleistocene finds of *C. c. crocuta* crania and lower jaws from a former collection are now spread to the private H. Hartnagel collection (=HH) and are from the HulunBuir region, Inner Mongolia, China. One mandible is from the 545km long Vilyuy River terraces near Tynda in Amur Oblast, Middle-East Siberia, Far East Russia, similar to other cranial material figured herein from other former collections (Figures 2–4). Several specimens were used from the recent e-bay portal and by photographs send by <https://ninjian.com/>, and www.henskensfossils.nl/ which “Siberian sites” were not mentioned there in some cases (Figures 2–5). Published Russian sites and their absolute data were compiled from the cited literature (cf. Tables 1 and 2).

Classical osteometric dental or cranial analyses have not resolved in the past the spotted hyena monophyletic lineage. There are several problems which have not been considered in former analyses: sexual dimorphism, strong cranial and mandibular shape variability, also dental variability if dental pathologies are present, strong worn teeth, and the most important problem, the mix of three distinct Pleistocene genera

Crocota, *Parahyaena* and *Hyaena* from Early to Middle Pleistocene Eurasian sites. Finally, the lack of international comparison to the older published European and younger presented Asian holotypes gave extraordinary confusion in the Pleistocene hyaenid taxonomy.

Herein, all Pleistocene holotypes including new rediscovered types are compiled from Europe, such as other important historic published cranial records (Figure 5). The crania and dentitions were compared directly to each other and the described Asian records, because all former statistics failed to resolve a clear evolution trend of the spotted hyenas *Crocota*. All tooth rows of those holotypes and other crania were scaled to similar lengths (Figure 5). The focus lies on the breaking scissor dentition and premolar accessory cone morphology such as M¹ development changes within the past 2.53 My (Figure 5).

Main and cladistic following character statistics, dental characters are classified herein in 1. Plesiomorph (conservative), 2. Intermediate and 3. Apomorph (advanced). These characters include: 1. P₂₋₃ proto- and paracone presence and size, 2. P⁴ length and paracone angle, and 3. M₁ presence or absence (reduction). Those characters are graphically and not statistically presented in Figure 5. Other relevant fossil Middle Pleistocene crania from Europe of *Parahyaena* and *Hyaena* are compared from different aged and the relevant sites Mas Cave in France (herein dated to MIS 15) and Mosbach open-air site, Germany (MIS 11). Stratigraphic well-dated material is used mainly, which allows placing and dating other insecure aged material, such as from the "Middle Pleistocene" site Mas Cave, France.

To understand the Siberian big game carcasses taphonomy (Figure 6), skin damage studies have been carried out at a monitored Zambian African *Loxodonta africana africana* that has been scavenged by hyenas (White & Diedrich, 2012). The available cited publication record of the Siberian mummified megafauna was first screened for any carnivore impact signs. For digital projection tests at the Siberian mummy skin cut signs, the redrawn spotted hyena dentition (occlusal views) of the new Inner Mongolian cranium and Siberian lower jaw records (Figures 2–4) are used.

4 | RESULTS AND DISCUSSION

4.1 | Pleistocene Eurasian spotted hyena and guilt coevolution

The monophyletic Mio-Pleistocene spotted hyena lineage is now followed back 12 Mio years ago into the Late Miocene. Material studied from the Samos site in the HLMD includes such a spotted hyena ancestor, which species had already strongly reduced M¹, which is a strong character in this genus (cf. Table 2), that continues in reduction with full absence in modern spotted hyenas. The taxonomy is confusing and incorrect for those oldest spotted hyenas. This not restudied Late Mio-Early Pliocene aged type specimen is furthermore named in its taxonomy to an own, but invalid genus "*Adrocota*" (Roth & Wagner, 1855; Koufos, 2011; Qiu, 1987). Clearly, two different hyena genera are recently found under the name "*A. eximia*." "*Adrocota*" represents indeed the genus *Crocota*, whereas "*eximia*" belongs, correctly identified by Roth & Wagner, 1855, to the genus *Hyaena*. *H. eximia* Roth and Wagner, 1854 (Roth & Wagner, 1855), was created based on a mandible that exhibits characters such as the very long and slim mandibular ramus are typical of *Hyaena* if compared to the herein new chosen extant *H. h. hyaena* skull holotype (UMM no. 168360). The Late Mio-Early Pliocene hyena cranium material from the Samos and Pikermi collections of the HLMD contain *Crocota* sp. At those sites, spotted hyenas already caused large guilt bone accumulations outside caves, which are generally not interpreted as such at non-human caused bone accumulation sites. Those spotted hyenas were unspecialized scavengers with a dentition still similar to *Parahyaena*, and *Hyaena*. Although the body size in the spotted hyenas' correlates to the proboscideans or elephants, the visible rapid dental modification of the spotted hyena teeth correlates to the climate and guilt change, about 805.000 years ago in the early Cromerian MIS 19 (first half of the Middle Pleistocene) (Figure 5).

For big game body cavity opening and removal of elephant, rhino or hippo body parts their heads, legs or vertebral

TABLE 2 *Crocota* tooth morphology characters and angle values of the crania (see Figure 5). Maxillary: 0 = Reduced, 1 = Small or shortest, 2 = Large or long, 3 = Largest or longest

Species	Time	P ² and P ₂		P ³ and P ₃		P ⁴	M ¹	M ₁
		Protocone	Paracone	Protocone	Paracone	Angle in °	Presence or absence	Total length
<i>C. c. crocuta</i>	MIS 1	0	0	0	0	112	0	3
<i>C. c. spelaea</i>	MIS 2–5d	0	0	0	0	112	0	3
<i>C. praespelaea</i>	MIS 5e11	1	1	1	1	112	1	2
<i>C. intermedia</i>	MIS 12–19	2	2	2	2	90	2	2
<i>C. brevirostris</i>	MIS 20–40	3	3	3	3	88	3	1

column parts—a very strong cutting scissor dentition had already started to develop in the Early Pleistocene *Crocota brevirostris* (Boule, 1893) (Figure 5). Compared to the younger spotted hyenas, the former *Pachycrocota* represents a still plesiomorphic toothed spotted hyena, which teeth were generally shorter, had larger accessory cusps, and the M^1 similar large but already typical in *Crocota* reduced in size similar as in the Pliocene forms. In contrast to the other two hyena genera, the breaking scissor dentition continued to evolve further to the Middle Pleistocene (MIS 19–12) *Crocota intermedia* (Serres et al., 1828). Indeed, the name *intermedia* is correct, because it shared the intermediate tooth characters between the older and younger *Crocota* species (cf. Table 2, Figure 5). It's to extant spotted hyenas closest apomorph characters are found within *C. praespelaea* (Schütt, 1971) which roamed Eurasia during the MIS 11–6 (Figure 5). Its dental characters bridge again between the older and younger aged species. In the Late Pleistocene MIS 5d, the last Eurasian Ice Age spotted hyena *Crocota crocuta spelaea* (Goldfuss, 1823) had evolved to the most efficient carnivore breaking scissor dentition with finally complete reduced M^1 much elongated M_1 and P^4 with high paracone angle for a longer cutting edge (Figure 5).

Within the past 805,000 years, the spotted hyena breaking scissor teeth P^4 and M_1 elongated in their cusps continuously. By the transition Middle to Late Pleistocene, the upper last molar M^1 had already no more space or function. Although the Eemian Interglacial Eurasian spotted hyenas still had a small M^1 , the MIS 5a-d records sometimes have, or sometimes do not have the M^1 which makes their attribution to the one or other species problematic (Figure 4). The pin-like tooth is found completely reduced at the end of the Late Pleistocene MIS 4–3 (Table 2). To this latest Late Pleistocene *C. c. spelaea* without M^1 , the new cranium from Hulun Buir region of Inner Mongolia, the cranium and jaws or Irkutsk and the lower jaws with long M_1 from Tynda region and other sites of Siberia and Russia to Mongolia (cf. Figures 2–4) all identify well to belonging to *C. c. spelaea*.

4.1.1 | *Crocota brevirostris* (Boule, 1893)—Giant spotted hyena

This formerly popular named “giant hyena” lived in the Early Pleistocene and beginning of the Middle Pleistocene MIS 104–19 (2.53 Mio. - 790,000 years ago) in Eurasia and Africa. It was binominal created based on a skull from Sainzelles near Le Puy of SW-France (cf. Boule, 1893) (cf. Figure 5). The validity of the holotype of Boule (1893) was not correctly discussed in Alba et al., (2015), because all historic French publications mentioned therein did not select a holotype, nor in the short note of Gervais 1850,

who finally also referred it incorrectly therein to a label that was mentioned by Aymard (cf. Gervais, 1848–1852). The latter did not present a binominal valid description in 1846 nor in further ones (cf. Gervais, 1848–1852). It was Boule in 1893 who again studied this material, in which he presented discussion and description such as skull illustration of “*Hyaena brevirostris*” (Boule, 1893) (cf. Figure 5) gave the taxon “validity.” This holotype of the herein to spotted hyenas belonging renamed *Crocota brevirostris* (Boule, 1893), based on its dental characters (cf. Table 2, Figure 5) comes from the Early Pleistocene (Late Villafranchien, around MIS 40, 1.3 Mio) megafauna assemblage, which is well known from several bone-rich sites in the Massif Central (Lacombat, 2005). Several of those French sites are solely in hyena communal den guilt accumulation den context (but not in early human), which were not described as such den sites. From this time of *C. brevirostris*, there are similar-aged hyena den guilt accumulation sites in Germany which have indeed at the Untermassfeld hyena den site (cf. Turner, 2001). *C. brevirostris* was spread between Asia all over Europe, for example to Spain, where those are also mainly in hyena guilt assemblage context (cf. Anton, 1996). Stratigraphic youngest finds added herein from the Czech Bat Cave, an early Mid-Pleistocene spotted hyena and wolf den, are dated by lithostratigraphy and micromammals (e.g. *Arvicula savini*) into the MIS 20 Interglacial. In China, this species received other names due to the lack of possible comparison to the European holotype, or confusion between three parallel living spotted, brown and striped hyena species (cf. Owen, 1870; Matsumoto, 1915; Huang, 1989). The non-valid Chinese “*C. ultima*” of Matsumoto, 1915 (single unstratified and not species characteristic tooth of hyaenid) from the Early Pleistocene to maximum early Middle Pleistocene could not have been found in MIS 8–3 as incorrectly described (cf. Baryshnikov, 2014). The monophyletic evolution model presented here does not support its believed age (cf. Figure 5). The single, not diagnostic P^4 occurred associated with a similar fauna, correlative to that of the Chinese Zhoukoudian *Homo erectus* site, which is dated most recently into the early Middle Pleistocene or early Cromerian Complex, MIS 20–18, respectively, 780,000–680,000 BP (Shen et al., 2009). This tooth has not to be relocated and must be revised to *C. brevirostris*, or a brown hyena *Parahyaena*. Herein, an undescribed nearly complete skull of *C. brevirostris* from Zhoukoudian Cave is added (Figure 5). Its material is similar in tooth morphology to the Schalksberg and Untermassfeld material from the MI 41 (Turner, 2001), or the Czech Bat Cave MIS 20. *C. brevirostris* was spread also all over Africa in the Early Pleistocene (Mutter et al., 2001), where it also used caves as dens similar to Eurasia populations, but in a lesser amount as Late Pleistocene spotted hyenas. Those

largest hyenas of our planet accumulated guilt remain at that time still more often in the open landscapes, similar to its Mio-Pliocene ancestors. At that time, there was heavy competition for cave use by different carnivore species or porcupines.

Craniodental characters of the Giant spotted hyena are found in their plesiomorph slim and elongated canines. The premolars are nearly identical to Mio-Pliocene forms with still more cutting function and larger accessory cusp cones, such as short breaking scissor teeth: M_1 and P^4 . The P^4 is plesiomorph with an angle of the proto- and metaconids below 90° (cf. Figure 5, Table 2), which is confusingly similar to *Parahyaena* (similar sized) and *Hyaena* (much smaller). There is one distinct character for this species in the lower jaw. The anterior part has, in comparison to all other hyaenids, a large height which gives the jaw a nearly lateral quadratic and massive outline. This shape also changed within the *Crocota* lineage to more triangle forms (Figure 5), which have the most massive part in the P_4 - M_1 area, here the highest pressure appears.

Those spotted hyenas coevolved into their most giant forms in correlation with the increase of the largest guilt elephant, *Elephas meriodonalis*, which both are present also at the French *C. brevirostris* type locality (Boule, 1893; Lacombat, 2005).

4.1.2 | *Crocota intermedia* (Serres et al., 1828)—Early Ice Age spotted hyena

It lived in the middle Middle Pleistocene, MIS 19–12 (676.000 – 478.000 years ago according to the chronostratigraphic absolute data of Lisiecki and Raymo (2005) [76], (Figure 5) in Eurasia and Africa. The most important European French site is Mas Cave near Lunel-Viel, which is dated herein by phylostratigraphic results into the MIS 15 Interglacial (cf. Figure 5). This age is further supported by the parallel presence of both interglacial hyenas: *Parahyaena* and *Hyaena*. *C. intermedia* was binominal named first in Europe 1828 based on the Mas Cave near Lunel-Viel hyena den as “*Hyaena intermedia*” (Serres et al., 1828) cranial and few postcranial materials (Serres et al., 1828). The historically and herein new figured cranium (Bonifay, 1970) 79] is chosen to represent the holotype specimen of *C. intermedia* (Serres et al., 1828) (cf. Figure 5). Former studies were mixing all three genera *Crocota*, *Parahyaena* and *Hyaena* at Mas Cave twice to a single species “*H. prisca*” (Serres et al., 1828). Although one “*H. prisca*” cranium was misidentified, representing instead *C. intermedia* (cf. Bonifay, 1970), only the mandible of *H. prisca* from the 1828 plates (cf. Bonifay, 1970) is the valid holotype to this extinct striped hyena. The nearly complete cranium published later by Bonifay (cf. Serres

et al., 1828) as *H. prisca* is chosen herein to represent the paratype to *H. prisca*. This is synonymous to the similarly aged early Cromerian Asian striped hyena records named as “*H. sinensis*.” The larger *Parahyaena* cranium from Mas Cave was also incorrectly named “*H. prisca*” (cf. Serres et al., 1828) and is placed herein preliminary to the few younger MIS 11 aged Mosbach brown hyena *P. b. mosbachensis* (Geib, 1915) (Reichenau, 1905; Geib, 1915). This forgotten type species and specimen with its cranial pathologic deformation have never been compared in studies of Asian material. Both striped and brown hyenas are similarly represented besides spotted hyenas at the late Cromerian site Mosbach (Reichenau, 1905; Geib, 1915; Schütt, 1971). Spotted hyenas dominate in the Cromerian site NISP numbers at both sites, Mas Cave and Mosbach, supporting the spotted hyena den site character. In the Cromerian Complex European and Asian those three hyaenids competed for parallel, but only in Interglacial periods in Europe.

Craniodental characters of the Early Ice Age spotted hyena are found in the plesiomorph, but less elongated and wider canines. There are many intermediate apomorph tooth characters at all P-M teeth (Table 2). The upper jaw P^{2-3} have already much more reduced accessory cones, whereas the still short P^4 measures around 90° in its plesiomorph para-metacone angle. The M_1 is intermediate in its length and between the sizes of *C. brevirostris* and *C. praespelae* (Table 2). Furthermore, both P_{3-4} have already starting apomorph accessory cone reduction at the premolars (cf. Figure 5).

Those spotted hyenas coevolved by no size decrease to the Eurasian steppe elephant *Elephas intermedius*, and large forest elephant *Loxodonta* sp., such as *Hippopotamus mayor* or the rhinoceroses with *Dicerorhinus etruscus*, *Stephanorhinus hundsheimensis* or *Stephanorhinus kirchbergensis* (cf. Figure 5), both are present, for example at the new studied Mosbach site within in the hyena guilt accumulation.

4.1.3 | *Crocota praespelae* (Schütt, 1971)—Old Ice Age spotted hyena

It was binominal valid established on a photographed and described maxillary of a cranium from the German Late Cromerian MIS 11 aged Mosbach Interglacial hyena den open-air site Mosbach along the Rhine River (cf. Schütt, 1971). This maxillary is now included in a complete cranium, that is figured here for the first time (Figure 5). Several younger aged Old Ice Age spotted hyena den cave sites in England of MIS 9 in age delivered the same subspecies with no further dental development (cf. Figure 5) (cf. Reynolds, 1902). This is known to be similar for

SE Asia, where it received different non-valid names in more recent publications (cf. Tseng & Chang, 2007; Jinyi et al., 2015; Kantapon et al., 2015). SE Asian and Russian Middle Pleistocene spotted hyenas were named “*C. c. ultima*” or “*C. c. ussurica*” without introducing convincing valid characters on a very incomplete cranium, including an incorrect differential diagnosis (cf. Baryshnikov, 2014; Jinyi et al., 2015). Those authors described indeed, as the phylostratigraphy and dental comparison presents herein (Figure 5), either *C. praespelaea* or *C. c. spelaea*. “*Hyaena ultima*” was created by Matsumoto, as mentioned earlier before for the Early Pleistocene-Middle Pleistocene boundary spotted hyena “*C. brevirostris*, in 1915” based on a non-diagnostic unclear aged P⁴, from the district of Szechuan, China (cf. Matsumoto, 1915; Huang, 1989).

Craniodental apomorph characters allow placing *C. praespelaea* possibly as subspecies as proposed by Schütt (1971), which cannot be confirmed by DNA for this old material, yet. The holotype cranium and other crania fragments from Mosbach (Figure 5) have a more reduced M¹, which pin-like tooth is only preserved at the Eemian Interglacial aged cranium from the Chinese Lingxiandong Cave (Jinyi et al., 2015) also incorrectly named there as “*C. ultima*.” Further incorrectly the cave was identified as communal den site, but it is a typical natal den with cub skeletons and a larger amount of natal den site characteristic nibbling bone sticks. The main criterion to separate this species from the last Ice Age spotted hyena is the length of the M₁ and P⁴ teeth, which places this species in-between the data of *C. intermedia* and *C. c. spelaea* (cf. Schütt, 1971). Distinct apomorph is now to *C. intermedia* the P⁴ with its much larger angle of about 110° (Table 2) as a result of tooth elongation for more efficient cutting function (Figure 6). The complete tooth length and its posterior part are still shorter, as in *C. c. spelaea* (cf. Schütt, 1971). Several crania added herein from the Hutton Cave (original of Reynolds (1902) or Torquay Cave and Kent’s Cavern hyena dens of southern England from the Holsteinian Interglacial MIS 9, share the same shorter breaking scissor dentition characters.

The correlation of coevolution between guilt size and spotted hyena size is similar to the aforementioned species. Spotted hyenas and elephants lived with remaining similar guilt megafauna. Largest elephants were still the steppe elephant *E. trogontherii*, but also *Loxodonta* sp., whereas several larger rhinoceroses were also present such as the most common *S. hundsheimensis* or large hippo *Hippopotamus mayor*. Spotted hyenas finally won after the MIS 9 in Eurasia the competition against most of their competing scavengers, such as last saber-tooth cat *Homotherium* such as *Parahyaena* and *Hyaena*. The Eurasian success and survival of Ice Age spotted hyenas lays also in the increased protection of cubs and guilt import in natural caves of mountain regions—which

other hyenas did not practice. *Parahyaena* and *Hyaena* den caves are not known for the Pleistocene of Europe, and if their remains are found in caves, those seem to be always in spotted hyena caused bone assemblages and must have been imported there, similar as other guilt including competing carnivores.

4.1.4 | *Crocota crocuta spelaea* (Goldfuss, 1823)—Ice Age spotted hyena

This first incorrectly named “cave hyena,” similar as a “cave wolf,” or “cave wolverine,” was found in the German Zoolithen Cave (Goldfuss, 1823). All of them were not cave inhabitants (Diedrich, 2014). This hyena was renamed in its popular name 2008 to “Ice Age spotted hyena” (Diedrich, 2008a). After biological ethospelologic terminology, those were subtrogliphiles and not permanent cave inhabitants, nor dependent on caves. They only used caves periodically as dens in different ways, and only in cave-rich karstic mountain landscapes (Diedrich, 2011b, 2014). Spotted hyenas are and were highly adaptable concerning their den choices and guilt sources. The last spotted hyenas of Eurasia populated in the Late Pleistocene MIS 5d-3 (113.000–24.000 years ago) and competed well in the open environment: mammoth steppe, boreal forests and even taiga landscapes of Siberia as we know now with the discoveries described herein. This by DNA tested subspecies (Rohland et al., 2005) was binominal named first in Europe 1823 by Goldfuss based on a cranium from the German Zoolithen Cave hyena and cave bear den as “*Hyaena spelaea*” (Goldfuss, 1823). This holotype original (cf. Figure 5) was lost for long period until its relocation in 2008 (Diedrich, 2008a), and again it was not included such as the new paratype (Diedrich, 2011b), in historic or newest Asian *Crocota* or other hyaenid studies (cf. Baryshnikov & Vereshchagin, 1996; Baryshnikov, 2014; Kosintsev et al., 2015; Kalmyko & Kobylkin, 2017). Craniodental, the extant spotted hyena characters are: fully developed braking scissor dentition with longest M₁ and P⁴ teeth such and the absence of M¹ since the MIS 4–3 (cf. Figures 2–5). A full reduction of the small upper jaw molar tooth M₁ seems to have happened within the MIS 5. The last crania of the MIS 3 generally do not have those fully reduced teeth anymore. However, it is in several crania of old to elderly increasing individuals increasing the difficulty to prove the presence or absence of the M¹. Often, those smallest teeth were damaged or lost quickly during a lifetime, and even the alveoli would close quickly, which gives a false picture of their original presence-absence. The absence of the M¹ of the paratype cranium of an adult from the Zoolithen Cave (cf. Figure 5) allows the dating into the MIS 4–3.

The new cranium from Inner Mongolia (Figure 2.1) is only in medium wear stage 1–2 and from an adult individual, where the open M^1 alveoli should be visible, or teeth present. Very obviously, there was no M^1 , which places the record into the MIS 3 best, from which most of the absolute dated frozen carcasses or skeletons from Siberia correlate in their ages (Popatova et al., 2018). The P^4 is also very long (58 mm) and falls into the uppermost lengths compared to German and Czech crania (cf. Diedrich, 2011b). The cranial convex sagittal crest shape type B has no taxonomic relevance (Diedrich, 2011a). This and the newer described herein to *C. c. spelaea* belonging revised crania from Geographical Society Cave (Baryshnikov, 2014), Oka Plateau (Kalmykov & Kobylkin, 2017) or Thailand (Kantapon et al., 2015), all with the absence of the M^1 , fall into the cranial variation of *C. c. spelaea*. The lower jaw and mandibles from the Middle-East Siberian Tynda, Irkutsk Region and other sites (cf. Figures 3–4) are by direct comparison to the European crania and mandibles all from *C. c. spelaea*, due to its long M^1 .

Since the MIS 5, Ice Age spotted hyenas no longer showed a decrease in size any longer, which lived along with the Eurasian woolly mammoth *Elephas (or Mammuthus) primigenius* and woolly rhinoceroses *Coelodonta antiquitatis* or steppe rhinoceros *Stephanorhinus hemitoechus* (e.g. Diedrich, 2013a, b) (cf. Figure 1d).

4.2 | Hyena palaeobiogeography and retreat-extinction model

The global northern hemisphere distribution of Ice Age spotted hyenas supports the idea of their retreat along with the megafauna at the end of the Ice Age to Siberia. The spotted hyenas reached or only remained longer in the Ural and Altai, also East Siberia and Mongolia such as China, Taiwan, and Thailand (cf. Figure 1d). The few short reports of the presence of those extinct spotted hyenas are from nine caves of the Ural (Baryshnikov & Vereshchagin, 1996), four caves in the Altai, and three caves of Far East Russia including the best-known Geographic Society Cave (Baryshnikov & Vereshchagin, 1996; Turner et al., 2001; Turner, 2010; Baryshnikov, 2014; Kalmykov & Kobylkin, 2017) (Table 1, Figure 1d). This mountain-limited presence indicated their possible more eastern and complete Eurasian extended palaeobiogeography. Newer finds of crania incorrectly described as different subspecies from China (Jinyi et al., 2015), Taiwan (Tseng & Chang, 2007) and Thailand (Kantapon et al., 2015) are revised to represent in most cases the same extinct Ice Age spotted hyena *C. c. spelaea*. Especially in mammoth steppe palaeoenvironments outside caves, those spotted hyena remains but there they are found similar rarely in Europe where they are found also generally with few records at open-air dens along river terraces (Diedrich, 2012a, 2013a, 2014).

European caves with more than 150 dens rarely contained complete skeletons, but more than 35 crania, mostly jaws, and many teeth and postcranial bones (Diedrich, 2014). Caves have been used by hyena clans as food storage, communal or birth dens. Badger-fox open-air burrows were reused as natal dens similar to known for extant African spotted hyenas which are known to compete with porcupines for the burrows (Diedrich, 2013a,b 2014). Those open-air localities are generally overlooked, more often destroyed by gravel pit activities, fluvial impact along rivers or their bone assemblages have not been identified to relate to the last bone crushers of Eurasia. In Siberia, selective bone collecting of the best value pieces destroyed the context for possible den site identifications. Fossil open-air dens were recently identified in Central Europe along rivers and lakes within loess and sandbank areas (Diedrich, 2012a, 2013a,b, 2014). Their remains with cranial dominance, cannibalistic damaged bones, coprolites for den marking and abundant guilt bones often with typical bite and chew damage—especially at more massive unbreakable woolly mammoth and woolly rhinoceroses' bones—are secure markers for their den areas (Diedrich, 2012a, 2013a,b, 2020a, 2020b).

The open landscape of Asia must have provided den sites for the now extinct spotted hyenas, but at this point of time unknown. First signs in Siberia for their dens or scavenging sites nearby dens within clan territories would contain damaged woolly mammoth and woolly rhinoceroses' bones. Such den marker bones have been found already all over Siberia, but are generally deselected not to be valuable for sale or taxonomic-morphologic research use. On the internet e-bay promoted mammoth and especially rhinoceroses' bones such a herein presented e-bay cranium with braincase opening (cf. Figure 6c) look completely similar in their damage patterns to European spotted hyena den site bone accumulation finds. Up to date, those Siberian carnivore damaged bones were not attributed to any hyena impact, nor taphonomic study focus.

4.3 | Siberian woolly mammoth and woolly rhinoceroses' scavengers

Bones of large elephant and rhinoceroses' carcasses have been damaged since the Miocene and Pleistocene by spotted hyenas which continued through the Pleistocene in Eurasia until today. Similar in elephants and rhinoceroses the giant guilt bones are filled by spongiosa and are unbreakable, even for best-adapted bone crushers (Diedrich, 2012a, 2013b, 2020b). Spotted hyenas can only chew their long bones and larger bones starting from soft distal joints, which always leaves similarly damaged bone shafts (Diedrich & Žák, 2006; Diedrich, 2008, 2012a,c,d, 2013a,b, 2017, 2020b). Bone breakage and flakes are known instead to occur from other prey groups such as bovids, cervids, equids, ursids and even their own species, which long bones are filled by bone marrow (Diedrich, 2008, 2011b,

2013a). Whereas the woolly mammoth record gives no clear indication of *C. c. spelaea* impact in Siberia as of yet, the situation is different in the woolly rhinoceros. This does not wonder, because in Europe it is well known, that *C. antiquitatis* was in the Late Pleistocene the second large and most important guilt in the mammoth steppe lowlands for the Ice Age spotted hyenas (Diedrich, 2013a,b, 2014). All Central European den sites nearby or within the lowlands share similar damaged rhinoceroses' bones that imply a systematic butchery techniques at scavenging sites (Diedrich, 2008, 2013a). Although no material of similar damaged long bones was available yet from Siberia, signs of cut-chew damage on the thick woolly rhinoceroses' skin were searched and confirmed found on some historically and newly discovered mummies.

4.3.1 | Kolyma rhino carcasses

A first, but not on the original full-studied mummy is the Kolyma bull (Figure 6a). In a former presentation of this on the International Mammoth conference 2010 the belly was presented visible from ventrally, which had along both skin sides zigzag margins. This open belly with mostly missing intestines and inner organs was briefly mentioned also in its description of 2011 (cf. Boeskorov et al., 2011). After the herein presented newer photograph, there are not only such irregular skin damages visible on the belly, but also on the right forelimb in the upper leg humerus-lower leg ulna-radius articulation elbow joint area (Figure 6a). The skin has bite impacts of canines and initial chew cuts left by the breaking scissor dentition. Here is where spotted hyenas started the disarticulation of the foreleg. A video of an African rhinoceros shows such a chew-cut scene on the foreleg. Very important are the European finds of consistent similar damaged woolly rhinoceros humeri (Diedrich, 2013a,b, 2014). The damaged humeri are always chew cut exactly in this joint area and are always missing only its outer lateral joint part. The Kolyma carcass helps to understand this humerus damage pattern. Hyenas butchered the carcass into body part pieces that were moved far to their dens, avoiding feeding conflicts with other hyena clans, lions or wolves packs (Diedrich, 2014). Skin remains from the Kolyma calf have again large round impacts and zigzag margins. The position in the anal region below the tail fits the aforementioned feeding strategy of both, lions and hyenas, starting feeding on this softer skinned part to reach most quickly the intestines. Impressive film sequences to such as feeding strategy are known from African elephant carcasses (Film 7) such as the monitored Zambian elephant carcass (White & Diedrich, 2012).

4.3.2 | Vilyuy River rhino carcass

The second and best proof for hyena scavenging damages on Siberian rhino carcasses is the historic mummy

find from the Vilyuy River (Brandt, 1849), which head was newly figured with a first photograph (Popatova et al., 2018) (Figure 6b). In historic illustrations of 1849 (Brandt, 1849), there are no signs of zigzag margins or any damages that would allow interpreting carnivore damage. This photograph shows strong, zigzag margins on the bone margin of the cranium, and the most secure bite chew cuts. Those are found in similar ways in the European bone record correlating to cut damage at the mandible ramus joint and zygomatic arch area (Figure 6b). Many European lower jaws were chewed and bite damaged exactly in this area for the lower jaw removal. Only on e-bay to study, several lower jaws and mandibles from Siberia are in the jaw joint area chew and bite damaged, and expose sometimes zigzag margins or large bite scratches and are missing the chew cracked joint area or ramus. The Vilyuy River carcass is the perfect example for initial head and lower jaw removal caused by spotted hyena scavenging activities. This is already known in the bone record at several Central European hyena den cave sites, where bite or chew-damaged crania or lower jaws were found in the guilt bone assemblages (Diedrich, 2008b, 2012a, 2013a, 2014). Secure identification of the hyena as a scavenger at this head comes from the digital projection tests of the premolar to molar dentition rows of both, lions and hyenas. Lions failed the projection in the upper and lower jaw dentition test. The skin has two places securely to identify the impact margins of the large oval-conical hyena P³ premolar tooth (Figure 6b). Instead, lions have elongated and flattened meat cutting premolars (Diedrich, 2013a,b, 2014). The P³ is the bone-crushing tooth within the premolar triangle crushing dentition which is behind the large cutting tooth, the P⁴ (Diedrich, 2014). Furthermore, the skin margin allows reconstructing perfectly and in the fossil record of frozen skin's unique chew-cut series. The upper hyena dentition produced the first three of in total six chew-cut bites in a row, whereas the last three are combined by the upper and lower jaw cutting scissors (Figure 6b).

The overlapping presence along the Vilyuy River in Middle Siberia of both, woolly rhinoceroses' guilt with its scavenger tooth signs, and Ice Age spotted hyena mandibles of *C. c. spelaea* (Figure 6b) have an impact on future taphonomic studies of the frozen mummies of Siberia. All past and future finds could be studied concerning large predator impact, especially at mammoths, to understand also their incompleteness as a result of the last Ice Age spotted Asian hyenas feeding strategies.

5 | Conclusions

The Pleistocene Ice Age spotted hyena has been revised based on the Eurasian cranial record, including the Asian

fossil studies and the forgotten European holotype crania and skulls, which all have been relocated in museums collections. The spotted hyena monophyletic lineage goes back 12 My ago. Within the past 2.53 Mio years, Pleistocene monophyletic lineage of *Crocuta* there was a coevolutionary adaptation to their largest thick-skinned elephant, rhinoceros and hippopotamus guild. Only the spotted hyena tooth morphology changed to the most efficient breaking scissor dentition perfect for thick skin cutting, whereas the other brown and striped hyena morphology remained more unspecialized.

The Eurasian and African Early to early Middle Pleistocene MIS 104–19 Giant spotted hyena *C. brevirostris* (Boule, 1893) is taxonomically valid not before 1893 based on the Late Villafranchian (around MIS 40) aged skull from Sainzelles, France. This still has a short last upper cutting P^4 , along with a well-developed but already small M_1 such as anteriorly high mandible and still slim canines. Those Giant spotted hyenas lived together with the largest elephant *E. meridionalis*.

Within the late middle Middle Pleistocene MIS 19–11, the Eurasian distributed Old Ice Age spotted hyena *C. intermedia* (Serres et al., 1828) is based on a cranium, a mandible being chosen herein, and other material from the French Mas Cave near Lunel-Viel. It already has a longer cutting scissor M_1 and P^4 such as now shorter and broader canine teeth. Furthermore, the additional conids of the P^{2-3} are more reduced. Its intermediate P^4 allows the dating of the Mas Cave hyena den bone assemblage between the MIS 19–12 of the middle Cromerian, most probably into the MIS 15 Interglacial. This is further supported by the parallel presence of Interglacial *Parahyaena* sp. and *Hyaena prisca* (Serres et al., 1828).

Already advanced is the latest Cromerian Mosbachian Interglacial MIS 11 *C. praespelaea* (Schütt, 1971) from the German Mosbach hyena open-air den site. This species used several caves in England as den sites such as other Eurasian caves in the MIS 9 Holsteinian Interglacial to finally MIS 5e Eemian Interglacial. Its dental characters, especially of the P^4 , are closer to the last Ice Age spotted hyenas. The P^3 is full conical developed as main bone puncture and crusher tooth. The small M^1 is still present.

The last fossil Ice Age spotted hyena *C. c. spelaea* (Goldfuss, 1823) with its holotype cranium and paratype skull from the German Zoolithen Cave from the MIS 5d-3 shows the final trend in dental adaptation to its important guild, woolly mammoth, and woolly rhinoceroses' thick skins and massive bones. The small M^1 is found to have been completely reduced secured in MIS 3 times, possibly reduced already before. To this latest *C. c. spelaea* from several European finds and the new Inner Mongolian and East Siberian lower jaws belong to. European and Asian crania fall with the Ural, Altai, Siberian, Chinese, Taiwan and Thailand

records into a single extinct northern hemisphere-wide distributed Late Pleistocene subspecies. There is non-taxonomic relevant variability in the cranial shapes with more flattened—type A—and with more convex—type B—sagittal crests forms in extinct and extant spotted hyenas, to which latter type B the Mongolian cranium refers to.

Ice Age spotted hyenas—historic and incorrect used the popular name "cave hyenas"—were not cave inhabitants. They are in the definition of modern biological ethological speleonomnclature troglophile (subtrogliphile) living animals. The main habitats were the mammoth steppe, boreal or leaf forest even up to taiga as we know now for Siberia. They hunted and scavenged any large game, which was imported in similar butchered body parts to open air or cave den sites. Caves were used only periodically for either commuting, as food storage and especially for cub raising as a natal den, similar to in extant African spotted hyenas. A Russian natal cave den of *C. c. spelaea* is identified for the Eastern Siberian Geographical Society Cave, where typical larger amounts of cub remain and their nibbling sticks for teething purposes have been found in the past, similar to the well described sites of the European Czech Bohemian Nad Kačakem Cave hyena natal cave. Modern spotted hyenas have more open-air den sites in Africa, simply as a result of cave-rich region absence. Other caves with concentrated hyena dens in the middle to the southern Ural, the Altai Mountains, and Far East Siberia allow mapping their distribution. Such den site maps are not reflecting their complete palaeobiogeography or palaeopopulation densities. As known for Europe, the open-air sites are still rare or are not identified. The newest Siberian—Mongolian—Chinese extinct Ice Age spotted hyena finds bridge now well European to East Siberia, the most Far East Russian records of the Geographical Society Cave and further south to the Taiwan and Thailand records.

Ice Age-spotted hyenas do have recently—due to the result of research history—their most dense finds in Europe, which are mostly dated into the Late Pleistocene MIS 5d-3. The fewer bone sites and bone amounts in the Ural, Altai, Mongolia and eastern Siberia date similar to herein identified scavenging sites often into the MIS 5d-3. Either the last bone crushers and big game thick skin cutters of Europe possibly retreated to Siberia together with their main and most important guild, the meat and bone colossus—woolly mammoth and woolly rhinoceros, or they simply survived longer in Asia correlating to the surviving of their meat and bone colossus guild into the Early Holocene period. Although in Europe the latest C^{14} dating gives an extinction for *C. c. spelaea* around 24.000 (MIS 3–2 boundary before the Last Glacial Maximum coldest period), it remains unknown, when the final spotted hyenas of Eurasia became extinct in Siberia. The coevolution between spotted hyenas and its main guild, the woolly rhinoceros, explains best their absence in North America.

The specialized thick skin-adapted breaking-cutting scissor dentition leaves for spotted hyenas only characteristic cut margins at elephants and rhinos' skins and bones. This indirect proof for their presence, similar damaged woolly rhinoceroses' skins, crania and especially postcranial long bones, are best markers for open-air den site identifications, which are now to be found in Siberia. First skin cut records are identified herein for frozen mummies, where hyena and not lion chew cutting signs are found on two woolly rhinoceroses' carcasses from the Kolyma and Vilyuy Rivers in Middle to East Siberia. The Kolyma bull was discovered without the inner intestines and organs, and with a long zig-zag margin cut on the belly, such as initial fore leg removal signs. The indirect hyena presence is furthermore obvious by the first and most eastern finds of a *C. c. spelaea* mandible and lower jaw, also coming from the Vilyuy River rhinoceros scavenging site area. Other Siberian cranial remains that are on sale on e-bay are also from unclear sites in Siberia. A first complete cranium and other cranial discoveries from Inner Mongolia and Mongolia such as China (cf. [https://ninijian.com/\(former coll. NIN\)](https://ninijian.com/(former coll. NIN))) extend the north-eastern Siberian presence of those top predators and their carcass impact on big game carcasses.

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CONFLICT OF INTEREST

The author has no competing interests.

AUTHOR CONTRIBUTION

The single author has carried out all the work.

RESEARCH ETHICS

None to declare.

DATA AVAILABILITY STATEMENT

All data are available in Tables 1 and 2. There are no datasets.

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REFERENCES

- Alba, D. M. A., Vinuesa, V., & Madurell-Malapeira, J. (2015). On the original author and year of description of the extinct hyaenid *Pachycrocuta brevirostris*. *Acta Palaeontologica Polonica*, *60*(3), 573–576.
- Anisimov, O. A., & Nelson, F. E. (1996). Permafrost distribution in the northern hemisphere under scenarios of climatic change. *Global and Planetary Change*, *14*, 59–72. [https://doi.org/10.1016/0921-8181\(96\)00002-1](https://doi.org/10.1016/0921-8181(96)00002-1)
- Apland, B., & Harington, C. R. (1994). Pleistocene bison skeleton (*Bison bison* cf. *occidentalis*) from Clayhurst Crossing, British Columbia. *Géographie Physique Et Quaternaire*, *48*(2), 213–223.
- Barnett, R., Shapiro, B., Barnes, L., Ho, S. Y. W., Burger, J., Yamaguchi, N., Higham, T. F. G., Wheeler, H. T., Rosendahl, W., Sher, A. V., Sotnikova, M., Kuznetsova, T., Baryshnikov, G. F., Martin, L. D., Harington, C. R., Burns, J. A., & Cooper, A. (2009). Phylogeography of lions (*Panthera leo* ss.) reveals three distinct taxa and a late Pleistocene reduction in genetic diversity. *Molecular Ecology*, *18*, 1668–1677.
- Baryshnikov, G. F. (2014). Late Pleistocene hyena *Crocuta ultima ussurica* (Mammalia: Carnivora: Hyaenidae) from the Palaeolithic site in Geographical Society Cave in the Russian Far East. *Proceedings of the Zoological Institute RAS*, *318*(3), 197–225.
- Baryshnikov, G. F. (2015). Late Pleistocene Ursidae and Mustelidae (Mammalia, Carnivora) remains from Geographical Society Cave in the Russian Far East. *Proceedings of the Zoological Institute RAS*, *319*(1), 3–22.
- Baryshnikov, G., & Boeskorov, G. (2001). The Pleistocene cave lion, *Panthera spelaea* Carnivora, Felidae) from Yakutia, Russia. *Cranium*, *18*, 7–24.
- Baryshnikov, G., & Vereshchagin, N. (1996). A brief review of Quaternary hyenas (Hyaenidae) of Russia and adjoining regions. *Trudy Zoologicheskogo Instituta RAN*, *270*, 7–65.
- Boeskorov, G. G., Lazerev, P. A., Sher, A. V., Davydov, S. P., Bakulina, N. T., Shchelchkova, M. V., Binladen, J., Willerslev, E., Buigues, B., & Tikhonov, A. N. (2011). Woolly rhino discovery in the lower Kolyma River. *Quaternary Science Reviews*, *30*(17–18), 2262–2272.
- Boeskorov, G. G., Protopopov, A. V., Maschenko, E. N., & Potapova, O. R. (2013). New findings of unique preserved fossil mammals in the permafrost of Yakutia. *Doklady Biological Sciences*, *452*(1), 291–295.
- Boeskorov, G., A. Tikhonov, & N. Suzuki (Eds.) (2007). *Yukagir Mammoth* (p. 252). Saint-Petersburg University Press.
- Bonifay, M. F. (1970). Carnivores Quaternaires du sud-est de la France. *Mémoires Du Muséum D'histoire Naturelle C*, *21*(2), 49–375.
- Boule, M. (1893). Description de l'*Hyaena brevirostris* du Pliocène de Sainzelles près le Puy (Haute-Loire). *Annales Des Sciences Naturelles Zoologie Et Paléontologie*, *7*(15), 85–97.
- Brandt, J. F. (1849). De Rhinocerotis antiquitatis seu tichorhini seu Pallassii structura externa et osteologica observationes e reliquisque in museis petropolitanis ser vanturerutae. *Mémoires De*

- L'Académie Impériale Des Sciences De St.-Petersbourg Sciences*, 1849, 161–416.
- de Serres, M. D. B., & Jeanjean, B. (1828). Recherches sur les ossements fossils des caverns de Lunel-Viel (Hérault). *Mémoires Du Muséum D'histoire Naturelle*, 17, 269–312.
- Diedrich, C. (2008a). The holotypes of the upper Pleistocene *Crocota crocuta spelaea* (Goldfuss, 1823: Hyaenidae) and *Panthera leo spelaea* (Goldfuss, 1810: Felidae) of the Zoolithen Cave hyena den (South-Germany) and their palaeo-ecological interpretation. *Zoological Journal of the Linnean Society London*, 154(4), 822–831.
- Diedrich, C. (2008b). Late Pleistocene hyenas *Crocota crocuta spelaea* (Goldfuss, 1823) from Upper Rhine valley open air sites and the contribution to skull shape variability. *Cranium*, 25(2), 31–42.
- Diedrich, C. (2010a). The *Crocota crocuta spelaea* (Goldfuss, 1823) population and its prey from the Late Pleistocene Teufelskammer Cave hyena den besides the famous Paleolithic Neandertal Cave (NRW, NW Germany). *Historical Biology*, 23(2–3), 237–270.
- Diedrich, C. (2010b). Periodical use of the Balve Cave (NW Germany) as a Late Pleistocene *Crocota crocuta spelaea* (Goldfuss, 1823) den: Hyena occupations and bone accumulations vs. human Middle Palaeolithic activity. *Quaternary International*, 233, 171–184.
- Diedrich, C. (2011a). One of Europe's last glacial *Crocota crocuta spelaea* (Goldfuss, 1823) clans from the Rösenbeck Cave hyena den (Germany) and contribution to cranial shape variability. *Biological Journal of the Linnean Society London*, 103, 191–220.
- Diedrich, C. (2011b). The Late Pleistocene spotted hyena *Crocota crocuta spelaea* (Goldfuss, 1823) population from the Zoolithen Cave at Gailenreuth (Bavaria, South Germany) – a hyena cub raising den of specialized cave bear scavengers in Boreal Forest environments of Central Europe. *Historical Biology*, 23(4), 335–367.
- Diedrich, C. (2012a). The Late Pleistocene *Crocota crocuta spelaea* (Goldfuss, 1823) population from the Emscher River terrace hyena open air den Bottrop and other sites in NW-Germany – woolly rhinoceros scavengers and their bone accumulations along rivers in lowland mammoth steppe environments. *Quaternary International*, 276(277), 93–119.
- Diedrich, C. (2012b). Late Pleistocene *Crocota crocuta spelaea* (Goldfuss, 1823) clans as przewalski horse hunters and woolly rhinoceros scavengers at the open air commuting den and contemporary Neandertal camp site Westeregeln (central Germany). *Journal of Archaeological Science*, 39(6), 1749–1767.
- Diedrich, C. (2012c). Europe's first Upper Pleistocene *Crocota crocuta spelaea* (Goldfuss, 1823) skeleton from the Koněprusy Caves - a hyena cave prey depot site in the Bohemian Karst (Czech Republic) - Late Pleistocene woolly rhinoceros scavengers. *Historical Biology*, 24(1), 63–89.
- Diedrich, C. (2012d). The Ice Age spotted *Crocota crocuta spelaea* (Goldfuss, 1823) population, their excrements and prey from the Late Pleistocene hyena den Sloup Cave in the Moravian Karst; Czech Republic. *Historical Biology*, 24(2), 161–185.
- Diedrich, C. (2013a). The Late Pleistocene spotted hyena *Crocota crocuta spelaea* (Goldfuss, 1823) open air birth and communal den site Bad Wildungen-Biedensteg (Hess, NW Germany) – woolly rhinoceros killers and scavengers in a mammoth steppe environment of Europe - ?recycling of badger/fox burrows in loess by hyenas in the Ice Age. *Journal of Geological Research*, 2013, 1–31.
- Diedrich, C. (2013b). Late Pleistocene Eemian hyena and steppe lion feeding strategies on their largest prey – *Palaeoloxodon antiquitatis* Falconer and Cautley, 1845 at the straight-tusked elephant graveyard and Neandertal site Neumark-Nord Lake 1, Central Germany. *Archaeological and Anthropological Sciences*, 6(3), 271–291.
- Diedrich, C. (2014). Palaeopopulations of Late Pleistocene top predators in Europe: Ice Age spotted hyenas and steppe lions in battle and competition about prey. *Paleontology Journal*, 2014, 1–34.
- Diedrich, C. (2017). Late Pleistocene hyena skeleton remains of a communal/prey depot cave den in the Bohemian Mountains (Czech Republic) - its osteology, taphonomy and palaeoecology. *Acta Zoologica*, 98(1), 66–93.
- Diedrich, C. (2020a). Eating head first - When European Ice Age spotted hyenas crushed their own to pieces. *Acta Zoologica*, 1–22. <https://doi.org/10.1111/azo.12323>
- Diedrich, C. (2020b). Top predators at war – Ice Age lions versus competing spotted hyenas. *Acta Zoologica*, 1–21. <https://doi.org/10.1111/azo.12345>
- Diedrich, C., & Žák, K. (2006). Upper Pleistocene hyena *Crocota crocuta spelaea* (Goldfuss, 1823) prey deposit and den sites in horizontal and vertical caves of the Bohemian Karst (Czech Republic). *Bulletin of Geosciences*, 81(4), 237–276.
- Eisenmann, V., & Sergej, V. (2010). Unexpected finding of a new *Equus* species (Mammalia, Perissodactyla) belonging to a supposedly extinct subgenus in late Pleistocene deposits of Khakassia (southwestern Siberia). *Geodiversitas*, 33(3), 519–530.
- Fisher, D. C. (2014). X-ray computed tomography of two mammoth calf mummies. *Journal of Paleontology*, 88(4), 664–675.
- Fisher, D. C., Tikhonov, A. N., Kosintsev, P. A., Rountrey, A. N., Buigues, B., & Plicht, J. (2012). Anatomy, death, and preservation of a woolly mammoth (*Mammuthus primigenius*) calf, Yamal Peninsula, north-west Siberia. *Quaternary International*, 255, 94–105.
- Geib, K. (1915). Zwei Arten von Streifenhyänen aus dem deutschen Diluvium. *Jahrbuch Des Nassauischen Verins Für Naturkunde*, 68, 2–20.
- Gervais, P. (1848–1852). *Zoologie et Paléontologie Françaises. Nouvelles Recherches sur les Animaux Vivants et Fossiles de la France*. Tome I. Contenant l'Énumération Méthodique et Descriptive des Espèces ainsi que les Principes de leur Distribution Géographique et Paléontologique. Arthus Bertrand Paris (pp. 1–271). <https://www.biodiversitylibrary.org/bibliography/39473#summary>
- Goldfuss, G. A. (1823). Osteologische Beiträge zur Kenntnis verschiedener Säugethiere der Vorwelt. VI. Ueber die Höhlen-Hyäne (*Hyaena spelaea*). *Nova Acta Physico-Medica Academiae Caesariae Leopoldino-Carolinae Naturae Curiosorum*, 3(2), 456–490.
- Guthrie, R. D. (1990). *Frozen Fauna of the Mammoth Steppe: The Story of Blue Babe* (pp. 323). Chicago: University of Chicago Press.
- Huang, W. P. (1989). Taxonomy of the Hyaenidae (*Hyaena* and *Crocota*) of the Pleistocene in China. *Vertebrata Palaeontologica Asiatica*, 27(3), 197–204.
- Jinyi, L., Wagner, J., Pingfu, C., Guilian, S., Jin, C., Qigao, J., & Sizhao, L. (2015). Mass mortality of a large population of the spotted hyenas (*Crocota ultima*) at the Lingxiandong Cave, Qinhuangdao, Hebei Province: a hyena communal den with its palaeoecological and taphonomical interpretation. *Quaternary Sciences*, 35(3), 607–621.
- Kalmykov, N. P., & Kobylkin, D. V. (2017). The first find of the cave hyena (*Crocota crocuta spelaea*) on the Oka plateau (Eastern Sayan). *Doklady Earth Sciences*, 477(1), 1247–1250.
- Kantapon, S., Yaowalsk, Y., Ajaeger, J. J., & Somsak, P. (2015). Complete skull of *Crocota crocuta ultima* indicates a late Middle Pleistocene age for the Khok Sung (north-eastern Thailand) vertebrate fauna. *Quaternary International*, 374, 34–45.

- Kirillova, I. V., Shidlovskiy, F. K., & Khasanov, B. F. (2011). First finding of a mammoth female (*Mammuthus primigenius* Blum.) on the Taimyr Peninsula. *Doklady in Earth Sciences*, 436(2), 193–196. <https://doi.org/10.1134/S1028334X11020152>
- Kirillova, I. V., Shidlovskiy, F. K., & Titov, V. V. (2012). Kastatyakh Mammoth from Taimyr. *Quaternary International*, 276–277, 269–277.
- Kirillova, I. V., Tiunov, A. V., Levchenko, V. A., Chernova, O. F., Yudin, V. G., Bertuch, F., & Shidlovskiy, F. K. (2015). On the discovery of a cave lion from the Malyy Anyui River (Chukotka, Russia). *Quaternary Science Reviews*, 117, 135–151. <https://doi.org/10.1016/j.quascirev.2015.03.029>
- Kirillova, I. V., Zanina, O. G., Chernova, O. F., Lapteva, E. G., Trofimova, S. S., Lebedev, V. S., Tiunov, A. V., Soares, A. E. R., Shidlovskiy, F. K., & Shapiro, B. (2015). An ancient bison from the mouth of the Rauchua River (Chukotka, Russia). *Quaternary Research*, 84, 232–245. <https://doi.org/10.1016/j.yqres.2015.06.003>
- Kosintsev, P. A., Gasilin, V. V., Gimranov, D. O., & Bachura, O. P. (2015). Carnivores (Mammalia, Carnivora) of the Urals in the Late Pleistocene and Holocene. *Quaternary International*, 420, 145–155. <https://doi.org/10.1016/j.quaint.2015.10.089>
- Koufos, G. D. (2011). The Miocene carnivore assemblage of Greece. *Estudios Geológicos*, 67(2), 291–320.
- Lacombat, F. (Ed.) (2005). Les grands mammifères fossiles du Velay. Les collections paléontologiques du Plio-Pléistocène du Musée Crozatier, Le Puy-en-Velay. *Annales Des Amis Du Musée Crozatier, 2004–2005*, 1–208.
- Lazarev, P. A. (2008). *Large Mammals of Anthropogene of Yakutia* (pp. 1–94). Moscow: Nauka.
- Lisiecki, L. E., & Raymo, M. E. (2005). A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}O$ records. *Palaeoceanography and Palaeoclimatology*, 20(1), 1–17.
- Lucas, F. A. (1898). The fossil Bison of North America. *Science New Series*, 8, 678.
- Maschenko, E. N., & Boeskorov, G. (2013). Morphology of a mammoth calf (*Mammuthus primigenius*) from Ol'chan (Oimiakon, Yakutia). *Paleontological Journal*, 47(4), 425–438.
- Maschenko, E. N., Gablina, S. S., Tesakov, A. S., & Simakova, A. N. (2006). The Sevska woolly mammoth (*Mammuthus primigenius*) site in Russia: Taphonomic, biological, and behavioral interpretations. *Quaternary International*, 142–143, 147–165.
- Maschenko, E. N., Potapova, O. R., Vershinina, A., Shapiro, B., Streletskaia, I. D., Vasiliev, A. A., Oblogov, G. E., Kharlamova, A. S., Potapov, E., van der Plicht, J., Tikhonov, A. N., Serdyuk, N. V., & Tarasenko, K. K. (2017). The Zhenya Mammoth (*Mammuthus primigenius* (Blum.)): Taphonomy, geology, age, morphology and ancient DNA of a 48,000-year-old frozen mummy from western Taimyr, Russia. *Quaternary International*, 445, 104–134. <https://doi.org/10.1016/j.quaint.2017.06.055>
- Maschenko, E. N., Protopopov, A. V., Plotnikov, V. V., & Pavlov, I. S. (2012). Specific features of the mammoth calf (*Mammuthus primigenius*) from the Khroma River (Yakutia). *Zoologicheskii Zhurnal*, 91, 1124–1140.
- Maschenko, E. N., Tikhonov, A. N., & MacPhee, R. D. E. (2005). Mammoth calf from Bolshoi Lyakhovskii Island (New Siberian Islands, Arctic Siberia). *Russian Journal of Theriology*, 4, 79–88. <https://doi.org/10.15298/rusjtheriol.04.1.06>
- Maschenko, E. N., Tikhonov, A. N., Serduk, N. V., Tarasenko, K. K., & Lopatin, A. V. (2015). A finding of a male mammoth carcass in the Karginsky suit of the Upper Pleistocene of the Taimyr Peninsula. *Doklady in Earth Sciences*, 460, 32–35.
- Matsumoto, H. (1915). On some fossil mammals from Szechuan, China. *Science Reports of the Tohoku Imperial University Ser 2 Geology*, 3, 1–28.
- Mol, D., Coppens, Y., Tikhonov, A. N., Agenbroad, L. D., MacPhee, R. D. E., Flemming, C., Greenwood, A., Buigues, B., Marliave, C., de Geel, B., van Reenen, G. B. A. van Pals, J. P., Fisher, D. C., Fox, D. (2001). *The Jarkov Mammoth: 20,000-Year-Old carcass of a Siberian woolly mammoth Mammuthus primigenius (Blumenbach, 1799)*. The World of Elephants, Proceedings of the 1st International Congress (16–20 October 2001, Rome), pp. 305–309.
- Mutter, R., Berger, L. R., & Schmidt, P. (2001). New evidence of the giant hyena *Pachycrocuta brevirostris* (Carnivora, Hyaenidae) from the Gladysvale Cave Deposit (Plio-Pleistocene, John Nash Nature Reserve, Gauteng, South Africa). *Palaeontologica Africana*, 37, 103–113.
- Nagaoka, D., Saijo, K., Fukuda, M., & Nakamura, T. (1996). Paleoenvironment and Period of The “Edoma” Formation in High Arctic Eastern Siberia. *Journal of Geography*, 195(1), 15–30. <https://doi.org/10.5026/jgeography.105.15>
- Novikov, B. V. (1993). *Wolverine* (p. 136). Lesnaya Promyshlennost.
- Owen, R. (1870). On fossil remains of mammals found in China. *Quarterly Journal of the Geological Society London*, 26, 417–434. <https://doi.org/10.1144/GSL.JGS.1870.026.01-02.40>
- Popatova, O., Shapiro, B., & Protopopov, A. (2018). Three centuries of hunting for ice age mummies and the prospect of de-extinction. *Palaeobiology*, 2018. <https://beta.capeia.com/paleobiology/2018/05/18/three-centuries-of-hunting-for-ice-age-mummies-and-the-prospect-of-de-extinction>
- Protopopov, A. V., Potapova, O. R., Kharmalova, A., & Klimovski, A. (2016). The frozen cave lion (*Panthera spelaea* (Goldfuss, 1810)) newborn cubs from Eastern Siberia, Russia: The first data on early ontogeny of the extinct species. *PA Journal of Vertebrate Paleontology, Program and Abstracts*, 2016, 209.
- Qiu, Z. X. (1987). Die Hyaeniden aus dem Ruscinium und Villafranchium Chinas. *Münchener Geowissenschaftliche Abhandlungen A*, 9, 1–108.
- Reynolds, S. H. (1902). A monograph of the British Pleistocene Mammalia. Volume II, Part II. The Cave Hyena. *Palaeontological Society Monographs*, 1902, 1–25.
- Rohland, N., Pollack, J. L., Nagel, D., Beauval, C., Airvaux, J., Paabo, S., & Hofreiter, M. (2005). The population history of extant and extinct hyenas. *Molecular Biology and Evolution*, 22(12), 2435–2443. <https://doi.org/10.1093/molbev/msi244>
- Roth, J., & Wagner, A. (1855). Die fossilen Knochen-Überreste von Pikerimi, Griechenland. *Abhandlungen Der Bayrischen Akademie Der Wissenschaften, mathematisch-naturwissenschaftlichen Klasse*, 7, 371–464.
- Russanov, B. S. (1968). Biostratigraphy of the Cenozoic sediments of southern Yakutia. *Nauk*, 1968, 1–458.
- Schütt, G. (1971). Die Hyänen der Mosbacher Sande (Altpleistozän, Wiesbaden/Hessen) mit einem Beitrag zur Stammesgeschichte der Gattung *Crocota* Mainzer. *Naturwissenschaftliches Archiv*, 10, 29–76.
- Séjourné, A., Costard, F., Fedorov, A., Gargani, J., Skorve, J., Massé, M., & Mège, D. (2015). Evolution of the banks of thermokarst lakes in Central Yakutia (Central Siberia) due to retrogressive thaw slump activity controlled by insulation. *Geomorphology*, 241, 31–40.
- Shen, G., Gao, X., Gao, B., & Granger, D. E. (2009). Age of Zhoukoudian *Homo erectus* determined with (26) Al/(10) Be burial dating. *Nature*, 458(7235), 198–200.

- Shpansky, A. V., Svyatko, S. V., Reimer, P. J., & Titov, S. V. (2016). Records of *Bison priscus* Bojanus (Artiodactyla, Bovidae) skeletons in Western Siberia. *Russian Journal of Theriology*, 15(2), 100–120. <https://doi.org/10.15298/rusjtheriol.15.2.04>
- Skinner, M. F., & Kaisen, O. C. (1974). The fossil Bison of Alaska and preliminary revisions of the genus. *Bulletin of the American Museum of Natural History*, 89, 123–256.
- Sokolov, V. E. (Ed.) (1982). *The Yuribei Mammoth* (pp. 1–122). Moscow: Nauka.
- Spasskaya, N. N., Kuznetsova, T. V., & Sher, A. V. (2012). Morphometric studies of the Late Pleistocene Bilibin horse mummy from western Chukotka Peninsula. *Paleontological Journal Moscow*, 1, 89–101.
- Tolmachoff, I. P. (1929). The carcasses of the mammoth and rhinoceros found in the frozen ground of Siberia. *Transactions of the American Philosophical Society*, 23(1), 11–23. <https://doi.org/10.2307/1005437>
- Tseng, Z. J., & Chang, C.-H. (2007). A study of new material of *Crocota crocuta ultima* (Carnivora: Hyaenidae) from the Quaternary of Taiwan. *Collections and Research*, 20, 9–19.
- Turner, A. (2001). Remains of *Pachycrocuta brevirostris* (Mammalia, Hyaenidae) from the Lower Pleistocene site of Untermassfeld near Meiningen. In H. D. Kahlke, & R. D. Kahlke (Eds.), *Das Pleistozän von Untermassfeld in Thüringen* (pp. 673–690). Rudolf Harbelt Verlag.
- Turner, A., & Antón, M. (1996). The giant hyaena *Pachycrocuta brevirostris* (Mammalia, Carnivora, Hyaenidae). *Geobios*, 29(4), 455–468. [https://doi.org/10.1016/S0016-6995\(96\)80005-2](https://doi.org/10.1016/S0016-6995(96)80005-2)
- Turner, C. G. (2010). The Russian-American perimortem taphonomy project in Siberia: A tribute to Nicolai Dmitrievich Ovodov, pioneering Siberian vertebrate paleontologist and cave archaeologist. *Alaska Journal of Anthropology*, 8(1), 87–105.
- Turner, C. G., Ovodov, N. D., Martynovich, N. V., Pavlova, O. V., Derevianko, A. P., & Drosdov, N. D. (2001). Perimortem bone taphonomy of late-Pleistocene human and hyena refuse deposits in Siberia. *Current Research in the Pleistocene*, 18, 88–90.
- Vasiliev, S. K. (2008). Late Pleistocene bison (*Bison priscus* Bojanus, 1827) from the southeastern part of Western Siberia. *Archaeology, Ethnology and Anthropology of Eurasia*, 34(2), 34–56.
- Vereshchagin, N. K. (1971). The cave lion and its history in the Holarctic and on the territory of the U.S.S.R. *Trudy of Zoological Institute Leningrad*, 49, 123–199.
- von Reichenau, W. (1905). Über einen Schädel der Hyaena arvernensis Croizet et Joubert aus dem Mosbacher Sande. *Jahresberichte Des Nassauischen Vereins Für Naturkunde*, 58, 177–182.
- White, P. A., & Diedrich, C. G. (2012). Taphonomy story of a modern African elephant *Loxodonta africana* carcass on a lakeshore in Zambia (Africa). *Quaternary International*, 276–277, 287–296. <https://doi.org/10.1016/j.quaint.2012.07.025>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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