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DANCING WITH WOLVES AT SCHÖNINGEN 13II-4

Abstract

The Schöningen 13II-4 site has produced a wealth of insight into the hunting and butchery activities of Middle Pleistocene hominins, highlighted by the famous Schöningen spears preserved with hundreds of cut-marked and broken horse bones. The bones of carnivores are rare at the site, but tooth pits, scores, and other markings that record their presence are abundant. Here we describe the carnivore remains from Schöningen 13II-4 and provide a detailed analysis of carnivore markings on different skeletal parts in the faunal assemblage and their spatial distribution. In studying carnivore activities at Schöningen, we aim to achieve a more comprehensive view of site taphonomy and, in turn, a better appreciation of the anthropogenic process that shaped the archaeological record. The placement and sequence of carnivore marks on the bones in relation to butchery marks indicates that carnivores scavenged from the remains of hominin kills. In the large horse bone assemblage, carnivore damage is more prevalent on limb bones of juveniles than adults. This pattern reveals that adult horse carcasses were fully butchered by hominins, but juvenile horse carcasses were abandoned earlier in the butchery process, leaving more consumable tissues that attracted scavenging carnivores. Tooth pits and scores on the Schöningen remains are very large and compare well with markings produced by wolves, especially those observed in a sample of modern wolf-gnawed bones we collected and analysed from *Adler- und Wolfspark* Kasteelburg. Clusters of carnivore-damaged bones appear around the periphery of dense concentrations of bones butchered by hominins, suggesting that wolves displaced some skeletal elements quickly after abandonment by hominins. Such a spatial pattern hints at the long-standing co-habitation of the Schöningen landscape by hominins and wolves during the Middle Pleistocene.

Keywords

Zooarchaeology, taphonomy, Middle Pleistocene, carnivores, wolf, cave lion

INTRODUCTION

The relationship between humans and carnivores is considered a major driving force in human evolution (Domínguez-Rodrigo, 2001). Hominin subsistence strategies increasingly focused on meat-eating have coincided with a reduced species richness in the African carnivore guild over the last two million years (Werdelin and Lewis, 2013), and it has been postulated that changes in the carnivore guild enabled early hominin dispersal into Eurasia (Lewis, 2017). Throughout the Middle and Upper Pleistocene, hominins and carnivores competed for similar resources, evidenced by the often alternating occupations of caves by either hominins or carnivores in archaeological contexts. Carnivores influenced the formation of many Pleistocene archaeological sites, either by contributing directly to the accumulation of faunal assemblages (Blumenschine, 1986; Bunn, 1989; Blumenschine and Selvaggio, 1991; Selvaggio, 1994; Stiner, 1994; Capaldo, 1995; Rosell and Blasco, 2009) or by scavenging the remains left behind by Palaeolithic hunters (Rosell and Blasco, 2009; Rosell et al., 2012). Humans were killed by large predators (Morel, 1998; Camarós et al., 2016; Daujeard et al., 2016), and sometimes their corpses were scavenged by carnivores (Stiner, 1991). On the other hand, carnivores were regularly hunted and exploited by humans (Kindler, 2012; Romandini et al., 2018; Cueto et al., 2020), for their fur (Auguste, 1995; Charles, 1997; Cueto et al., 2016), for their teeth to

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use as personal ornaments (Wojtal et al., 2020), for bait (Street and Turner, 2013), or to domesticate them (Street et al., 1989; Chaix et al., 1997; Street et al., 2015). Consequently, an understanding of the evolving relationship between humans and carnivores helps to define the human niche and to evaluate the circumstances under which hominins proactively influenced and altered their position in the food web throughout the Pleistocene.

Especially for Middle Pleistocene contexts, accounting for the role carnivores played in the formation and preservation of archaeological sites can provide for a more holistic view of Palaeolithic hunter-gatherer subsistence strategies (Blasco and Rosell, 2009; Gaudzinski-Windheuser and Niven, 2009; Starkovich and Conard, 2020). In this context, it is of particular interest to interrogate key archaeological sites with outstanding preservation and in undisturbed contexts, such as the site of Schöningen 13II-4. The open-air, lakeshore site of Schöningen 13II-4, most famous for the wooden spears and butchered horses, also preserved the remains of several large carnivores and a significant number of ungulate bones showing traces of carnivore activity, such as tooth pits and other damage from gnawing (Thieme, 2005; Voormolen, 2008; van Kolfschoten, 2014; van Kolfschoten et al., 2015; Hutson et al., 2020). Schöningen 13II-4 has provided a wealth of information about Middle Pleistocene hominin lifeways and likewise has great potential to inform on the position of hominins within the carnivore community during the European Middle Pleistocene.

Here we present an analysis of the carnivore remains and other evidence for carnivore activity from Schöningen 13II-4. We contextualize our zooarchaeological and taphonomic analyses within the wider European Middle Pleistocene carnivore community in order to formulate a potential cast of carnivore actors present

Fig. 1 Map of Germany showing the location of Schöningen and other sites mentioned in the text with carnivore faunal remains.

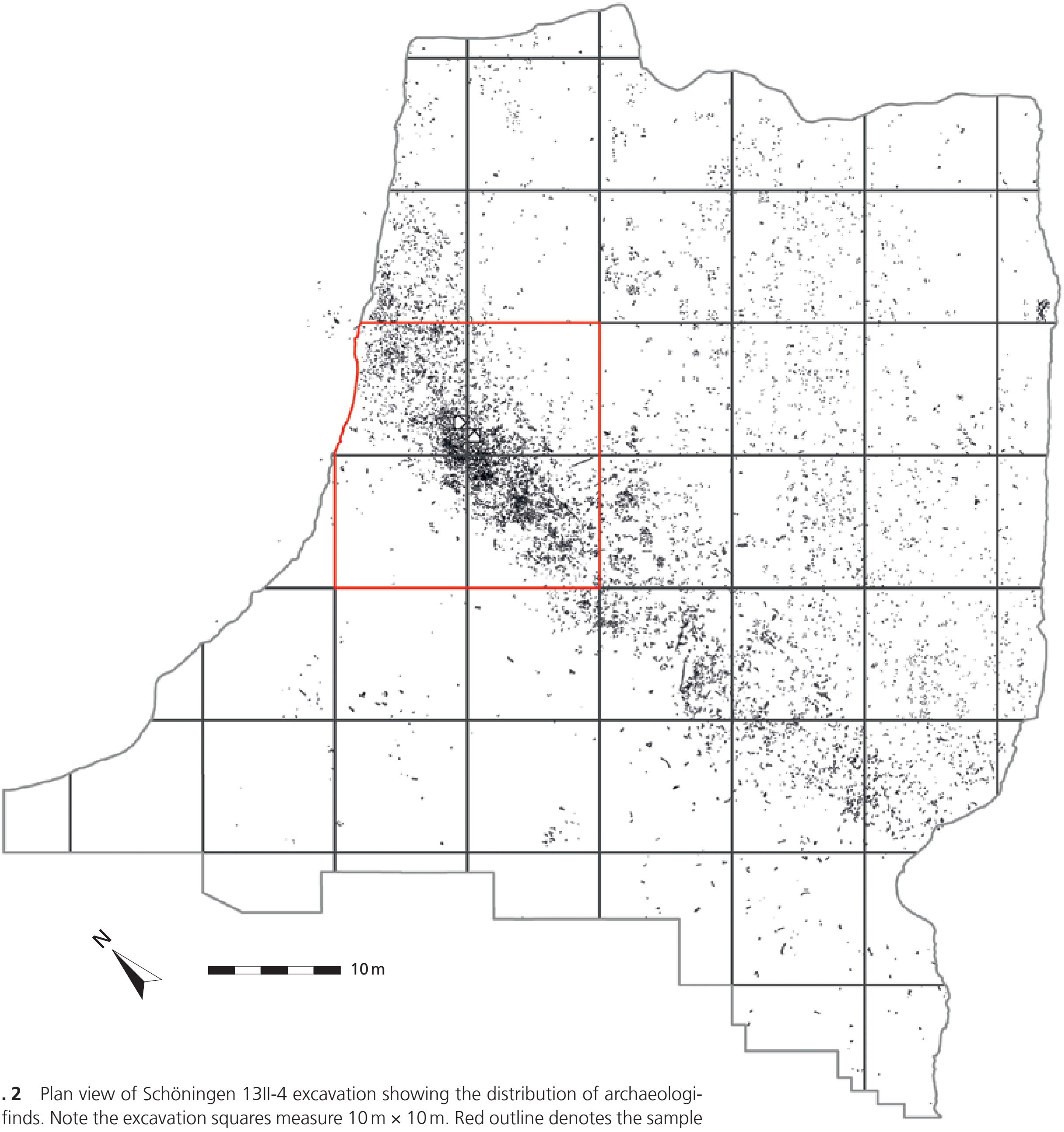


Fig. 2 Plan view of Schöningen 13II-4 excavation showing the distribution of archaeological finds. Note the excavation squares measure 10 m × 10 m. Red outline denotes the sample area for all measured carnivore tooth pits, punctures, and scores.

on the Schöningen landscape. Actualistic studies, in addition to a thorough review of known patterns of carnivore damage to ungulate bones, were employed to further identify the carnivore species involved in modifying the Schöningen faunal assemblage. Lastly, we introduce an in-depth spatial analysis to better understand the taphonomic history of the Schöningen deposit and temporal relationships between hominins and carnivores at the site. Altogether, our aim is to detail the role of carnivores in the formation of this important archaeological site, and more broadly, bring into focus the relationship between hominins and carnivores during the Middle Pleistocene.

Fig. 3 (Top) Wolf in one of the large wooded enclosures at the *Adler- und Wolfspark* Kasteelburg. (Bottom, left to right) *Bos taurus* radius, femur, and tibia gnawed by wolves from Wolfspark Kasteelburg.

SITE BACKGROUND

Open-cast mining activity near the town of Schöningen (Lower Saxony, Germany; **Fig. 1**) led to the discovery of a series of archaeological sites contained within a sequence of erosional 'channels' dating from the Middle Pleistocene (Serangeli et al., 2012). These 'channels' indicate the presence of a large paleo-lake. The site named Schöningen 13II-4 (site 13, channel II, level 4) became known worldwide in the 1990s as the 'Spear Horizon', due to the extraordinary discovery of several wooden spears (Thieme, 1997, 2007; Schoch et al., 2015) alongside an archaeological assemblage of around 15,000 faunal remains, 1,500 lithics, and a significant number of wooden and other macro-botanical remains (Serangeli and Böhner, 2012). Excavations by Hartmut Thieme from 1995 to 2008 extended over an area of 3,900 m^2. The exceptionally preserved faunal assemblage, mainly composed of horse bones, was originally interpreted as the remains of a mass-kill hunting event near the lakeshore and dated to around 400 ka (Thieme, 2005). However, both the interpretation and chronology of the site were challenged by later studies, which demonstrated that the site formed through the accumulation of several hunting events (Voormolen, 2008; van Kolfschoten, 2014; Julien et al., 2015b; van Kolfschoten et al., 2015; Hutson et al., 2020) during Marine Isotope Stage 9 (MIS 9; Richter and Krbetschek, 2015) or a later interglacial period.

Multiple geological and paleoenvironmental records (Lang et al., 2012, 2015; Stahlschmidt et al., 2015; Peters and van Kolfschoten, 2020; García-Moreno et al., 2021) indicate the Schöningen 13II-4 site formed in a delta lacustrine environment straddling the dryland, shoreline, and shallow water zones of the Schöningen paleo-lake. The lake was surrounded by a mosaic landscape, with aquatic plants at the lake margins surrounded by grassland and open forest (Urban and Bigga, 2015; Bigga, 2018). The 'Spear Horizon' was embedded in the uppermost 30-40 cm of the sedimentary sequence of Level 4. Most of the archaeological remains appeared in sublayer 4b, a dark brown laminated organic silt layer. Actualistic experiments revealed that black staining on many of the faunal remains was caused by decaying plant in waterlogged sediments (Turner et al., 2018). Consequently, the Schöningen 13II-4 site likely formed in the shallow waters of the lakeshore and nearby swampy areas. Roughly two-thirds of the archaeological assemblage is distributed along a 10 m wide by 60 m long strip extending north-to-south across the site (**Fig. 2**). This concentration is interpreted as a close approximation of the shoreline during major episodes of hominin activity (Böhner et al., 2015; García-Moreno et al., 2021), with permanently dry land to the west and the deeper portion of the lake basin to the east. Faunal remains are significantly more scattered throughout the eastern portion of the site, which may correspond to deposition during periods when the lake level was lower (Turner et al., 2018; García-Moreno et al., 2021). Based on sediment micromorphology, orientation of archaeological finds, and other taphonomic indicators, there is no evidence of significant post-depositional alterations of the assemblage (Böhner et al., 2015; Stahlschmidt et al., 2015; Turner et al., 2018; Hutson et al., 2020; Peters and van Kolfschoten, 2020; García-Moreno et al., 2021).

The Schöningen 13II-4 faunal assemblage consists of roughly 15,000 remains, nearly all of which is derived from the 'Spear Horizon' (García-Moreno et al., 2021). Horse (*Equus mosbachensis*) is overwhelmingly abundant, represented by 9,018 identifiable specimens (NISP – number of identified specimens). Red deer (*Cervus elaphus*) is the next most abundant taxon, yet only numbers 358 NISP. Two bovid species, the steppe bison (*Bison priscus*) and aurochs (*Bos primigenius*), are represented by a combined 289 NISP. Other ungulate species are present at Schöningen 13II-4 in low numbers, including the European wild ass (*Equus hydruntinus*), roe deer (*Capreolus capreolus*), giant deer (*Megaloceros giganteus*), straight-tusked elephant (*Palaeoloxodon antiquus*), and two rhinoceros species (Welker et al., 2017): narrow-nosed rhinoceros (*Stephanorhinus hemitoechus*) and Merck's rhinoceros (*Stephanorhinus kirchbergensis*). Other small mammals, birds, fish, and amphibians are present in the Schöningen 13II-4 faunal assemblage (Voormolen, 2008; Böhme, 2015; van Kolfschoten et al., 2015; Hutson et al., 2020; García-Moreno et al., 2021). The various carnivores and traces left by carnivores on the ungulate bones are reported in detail here.

MATERIALS AND METHODS

This account of the Schöningen carnivores constitutes part of an ongoing analysis of the complete faunal assemblage from the Schöningen 13II-4 deposit. A full account of our zooarchaeological and taphonomic methodology is provided in Hutson et al. (2020). Taxonomic identifications were made using the comparative collection housed at the MONREPOS Archaeological Research Centre and Museum for Human Behavioural Evolution. Identifications were made at the species level when possible, otherwise minimally identifiable specimens were categorized by size (e.g., red deer-sized, horse-sized, bison/aurochs-sized). Standardized anatomical measurements of individual carnivore skeletal parts were taken with digital callipers following von den Driesch (1978). Taxonomic and skeletal part abundances herein are based on number of identified specimens (NISP).

Taxon	ID #	Bone	Side	Portion
Canis lupus, Wolf	18835	Radius	Left	Complete
NISP = 7	11711	Innominate	Right	Incomplete
	20637	Innominate	Right	Ilium + acetabulum
	3781	Femur	Right	Shaft
	21099	Femur	Left	Proximal
	20330.1	Tibia	Left	Shaft
	15693	Lumbar vertebra	-	Dorsal
Vulpes vulpes, Red fox	11600	Maxilla (C, P1, P3, P4)	Left	Incomplete
NISP = 3	19099.1	Rib	Indet.	Shaft
	21098	Tibia	Left	Distal + shaft
Meles meles, European badger	11929	Ulna	Left	Complete
NISP = 5	15697	Cervical vertebra	-	Cranial
	15711	Rib	Indet.	Shaft
	19023	Ulna	Right	Proximal
	19574	Innominate	Left	Acetabulum
Mustela sp., Weasel	2243	Innominate	Right	Ischium + acetabulum
NISP = 5	2463	Caudal vertebra	-	Complete
	2463.1	Limb	Indet.	Shaft
	10190.2	Phalange	Indet.	Complete
	21162.7	Metapodial	Indet.	Complete
cf. *Panthera leo spelaea*, Cave lion NISP = 1	11440	Thoracic vertebra	-	Incomplete
Carnivora indet., Large carnivore	1279	Rib	Indet.	Shaft
NISP = 4	2834	Rib	Indet.	Shaft
	4159.3	Rib	Indet.	Shaft
	19691.1	Coprolite	-	Fragment

Tab. 1 Schöningen 13II-4 carnivore species list and description of skeletal remains.

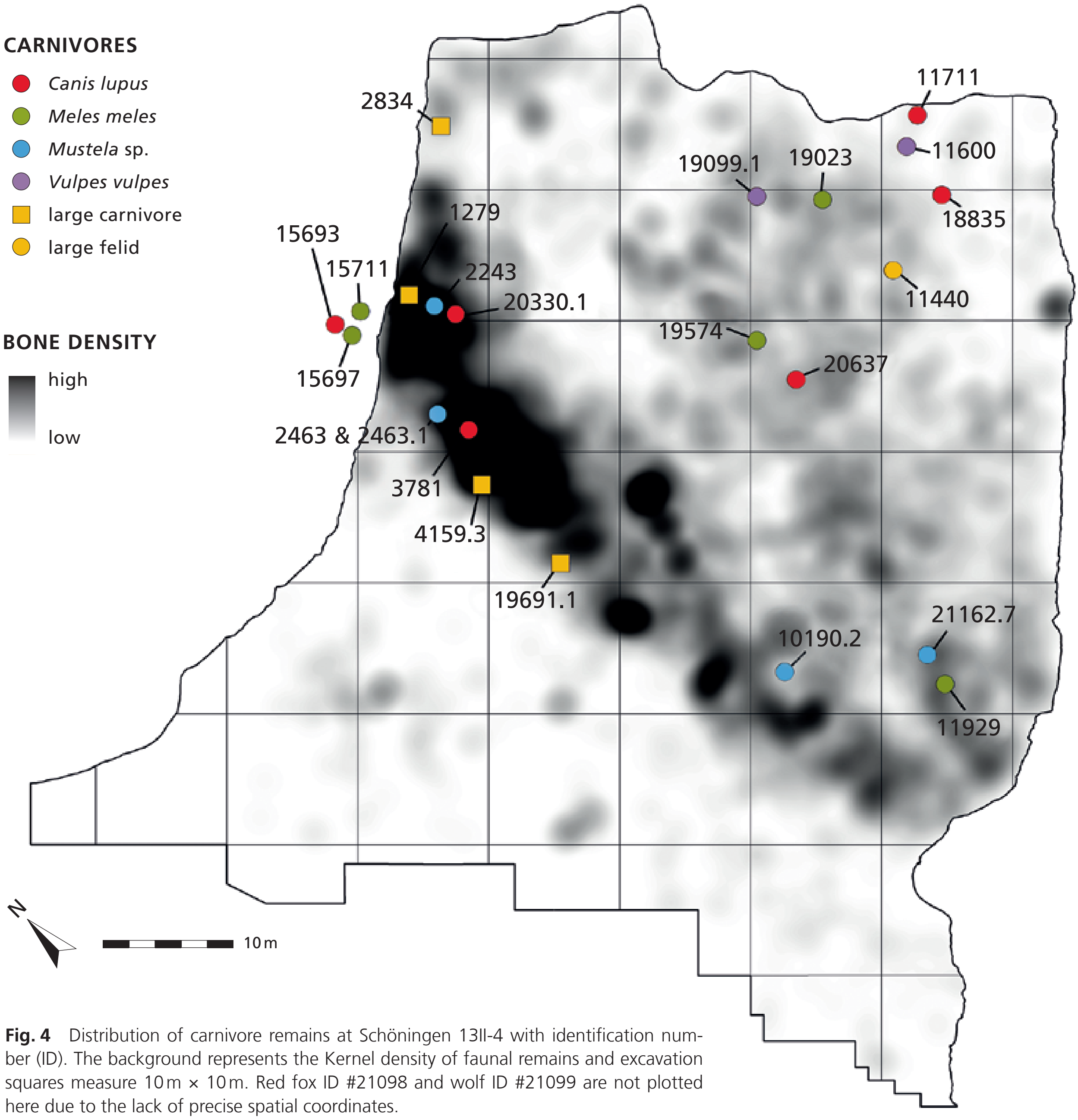


Fig. 4 Distribution of carnivore remains at Schöningen 13II-4 with identification number (ID). The background represents the Kernel density of faunal remains and excavation squares measure 10 m × 10 m. Red fox ID #21098 and wolf ID #21099 are not plotted here due to the lack of precise spatial coordinates.

All bones were examined under magnification with a 10x hand lens or 20-40x digital microscope for surface modifications. Of primary interest here is damage produced by carnivore teeth during feeding, and identifications of all carnivore traces, notably tooth pits, punctures, and scores, were based on descriptions and images provided by various taphonomic manuals (e.g., Lyman, 1994; Fisher, 1995; Fernández-Jalvo and Andrews, 2016; Gifford-Gonzalez, 2018), and specifically outlined in Lehnig et al. (2021). Importantly, pits were distinguished from punctures in that punctures penetrate the cortical surface, whereas pits do not; pits were distinguished from scores in that score length is greater than or equal to three times the breadth, whereas pit length is less than three times the breadth. The locations of carnivore modifications (also hominin butchery marks) were marked in digital templates of individual skeletal elements and compiled using a GIS approach (García-Moreno et al., 2015). Length and breadth measurements of pits, punctures, and

Site	Location	Age	Species	Radius	Femur		Reference
				Greatest length (GL)	Greatest breadth of proximal end (Bp)	Greatest depth of caput femoris (DC)	
Untermaßfeld	Germany	~1 Ma	*Canis mosbachensis*	163.0-169.0 n = 4	34.7-39.5 n = 7		Sotnikova, 2001
Escale	France	800-700 ka	*Canis mosbachensis*	151.5-174.6 n = 20	32.4-41.0 n = 14	16.0-19.0 n = 14	Boudadi-Maligne, 2011
Igue des Rameaux	France	MIS 11/10	*Canis lupus*	155.4-174.6 n = 7	39.1-47.0 n = 9	17.9-23.0 n = 14	Boudadi-Maligne, 2011
Lunel Viel I	France	~400-350 ka	*Canis lupus*	171.0 n = 1			Boudadi-Maligne, 2011
Schöningen	**Germany**	**MIS 9**	***Canis lupus***	**190.9** **n = 1**	**47.0** **n = 1**	**21.3** **n = 1**	**present study**
Coudoulous I	France	MIS 7	*Canis lupus*	178.9 n = 1	44.0 n = 1	20.4-20.7 n = 3	Boudadi-Maligne, 2011
Malarnaud	France	MIS 5	*Canis lupus*	190.0-213.0 n = 3	46.0-53.5 n = 4	24.0-25.0 n = 4	Dufour, 1989
Aven de l'Arquet	France	MIS 3 (40 ka)	*Canis lupus*	183.3-207.9 n = 4	47.0-53.5 n = 5	23.0-26.2 n = 8	Boudadi-Maligne, 2011
Jaurens	France	MIS 3 (30 ka)	*Canis lupus*	217.3-218.8 n = 2	58.1 n = 1	27.2-27.2 n = 2	Boudadi-Maligne, 2011
Maldidier	France	MIS 3 (30 ka)	*Canis lupus*	212.6-222.6 n = 3			Boudadi-Maligne, 2011

Tab. 2 Anatomical comparison between wolf remains from Schöningen 13II-4 and other Pleistocene sites. All measurements (in mm) follow von den Driesch (1978).

scores from a sample of the Schöningen material were taken with digital callipers directly on the marks following Andrés et al. (2012).

The measured sample is drawn from the area of the site with the densest concentration of faunal remains, covering roughly 40 m^2 at the northern end of the main accumulation (see **Fig. 2**). The sample area includes a total 5,391 faunal remains (37.2 % of the overall assemblage); 71 limb bones and limb bone fragments of horse, red deer, and bison/aurochs from this sample preserved evidence of carnivore damage, and we measured 186 tooth pits and 179 tooth scores from the Schöningen sample.

Measurements of carnivore tooth pits and scores have been used with varying success to identify the species responsible for modifying faunal assemblages, and measurements of pits and scores on a sample of the Schöningen material were compared to similar marks on bones fed on by a number of carnivore species during actualistic or experimental studies, including wolf (*Canis lupus*), dog (*Canis familiaris*), coyote (*Canis latrans*), black-backed jackal (*Canis mesomelas*), red fox (*Vulpes vulpes*), brown bear (*Ursus arctos*), spotted hyena (*Crocuta Crocuta*), African lion (*Panthera leo*), mountain lion (*Felis concolor*), and bobcat (*Lynx rufus*) (see Domínguez-Rodrigo and Piqueras, 2003; Campmans and Beauval, 2008; Delaney-Rivera et al., 2009; Andrés et al., 2012; Sala, 2012; Saladié et al., 2013; Sala et al., 2014; Young et al., 2015; Yravedra et al., 2019). Individually, these published studies encompass a range of experimental methodologies, involving wild, captive, and domesticated animals feeding on large and small ungulate bones. Furthermore, most of

Fig. 5 Cranial view of a wolf (*Canis lupus*) left radius (ID #18835) from Schöningen 13II-4.

Fig. 6 Cranial view of an incomplete large felid (cf. *Panthera leo spelaea*, cave lion) thoracic vertebra (ID #11440) from Schöningen 13II-4.

Fig. 7 Horse (*Equus mosbachensis*) right innominate (ID #7191) gnawed by carnivore. Note the scalloped edge and multiple tooth punctures.

these studies differentiated between marks located on limb bone mid-shafts (diaphyses), near-epiphyses (metaphyses), and ends (epiphyses) because the dimensions of carnivore tooth pits and scores could be affected by bone density, i. e., carnivores impart longer and broader pits and scores on the less dense epiphysis portions of long bones. These divisions result in small sample sizes for some carnivore species. To increase sample sizes, we pooled all studies together by species using published data on mean, standard deviation, and individual sample size of the length and breadth measurements of tooth pits and scores, with no regard to the location of the marks (i. e., diaphysis, metaphysis, epiphysis). Punctures were also included with the measurements of pits. This greatly increased the sample sizes for nearly all species involved for comparison against the sample of pits and scores from the Schöningen assemblage.

To this, we add our own collection of wolf-modified bones gathered from *Adler- und Wolfspark* Kasteelburg (Germany; **Fig. 3**). *Adler- und Wolfspark* Kasteelburg hosts semi-wild 'arctic' and 'timber' wolves in two separate forested enclosures covering 20 ha. The pack of 'timber' wolves is fed portions of animal carcasses on a regular schedule and the discarded bones are generally left within the enclosure after feeding, perhaps for a period of up to several years. During a walking survey of the 'timber' wolf enclosure in June 2014, we gathered 167 bones (scapula, humerus, radius, ulna, femur, tibia, and metapodials), mostly from cow (*Bos taurus*), horse (*Equus caballus*), and sheep (*Ovis aries*), the occasional roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*), and possibly red deer (*Cervus elaphus*). All bones were well-preserved and unweathered when recovered owing to the protective cover of the forested environment. In total, we identified and measured 249 pits (including punctures) and 1,067 scores from the *Adler- und Wolfspark* collection, which is currently housed at the MONREPOS Archaeological Research Centre and Museum for Human Behavioural Evolution and available for study.

Differences in length and breadth measurements of pits and scores between the pooled carnivore samples and the Schöningen sample were calculated using independent t-tests.

As the foundation for spatial analysis, all faunal remains were plotted according to their three-dimensional coordinates based on the local reference system of the excavation grid. Of particular relevance here are the precise locations of carnivore remains and other faunal remains modified by carnivores and hominins. In cases where precise coordinates were not recorded during field excavations, artificial coordinates were given to those finds using the central point of the corresponding 1 × 1 m². Once plotted, the mean, minimum, and maximum distance between carnivore remains was calculated. In order to visualize the spatial patterning of the remains showing butchery traces and carnivore damage, Kernel density estimates were analysed. Based on this, areas showing densities of butchered bones higher than the mean density were defined; likewise, areas with densities of bones affected by carnivores higher than the mean were defined. Superimposing the high-density butchery areas with the high-density carnivore areas allows for the identification of zones where hominin and carnivore activities are spatially exclusive and where those activities overlap.

The distribution of butchered and carnivore-damaged bones is, in part, influenced by the overall spatial patterning of faunal remains across the site. Here we define and calculate a Carnivore/Butchery Index (CBI) to evaluate whether bones showing butchery marks or carnivore damage were more abundant per area unit. First, we used the Quadrat method to estimate the cell size of a regular grid that best fits the dimensions of the site and number of finds (Getis, 1964; Sánchez Romero, 2019). Based on that, we created an ‘improved’

Fig. 8 Horse (*Equus mosbachensis*) left rib (ID #5534) gnawed by carnivore. Note the scalloped margin and tooth score at the distal end.

Fig. 9 Horse (*Equus mosbachensis*) right ulna (ID #1374) gnawed by carnivore. Note the scalloped edge on the proximal end.

Fig. 10 Subadult horse (*Equus mosbachensis*) left humerus (ID #5484) gnawed by carnivore. Proximal and distal ends have been completely gnawed, leaving bone cylinder.

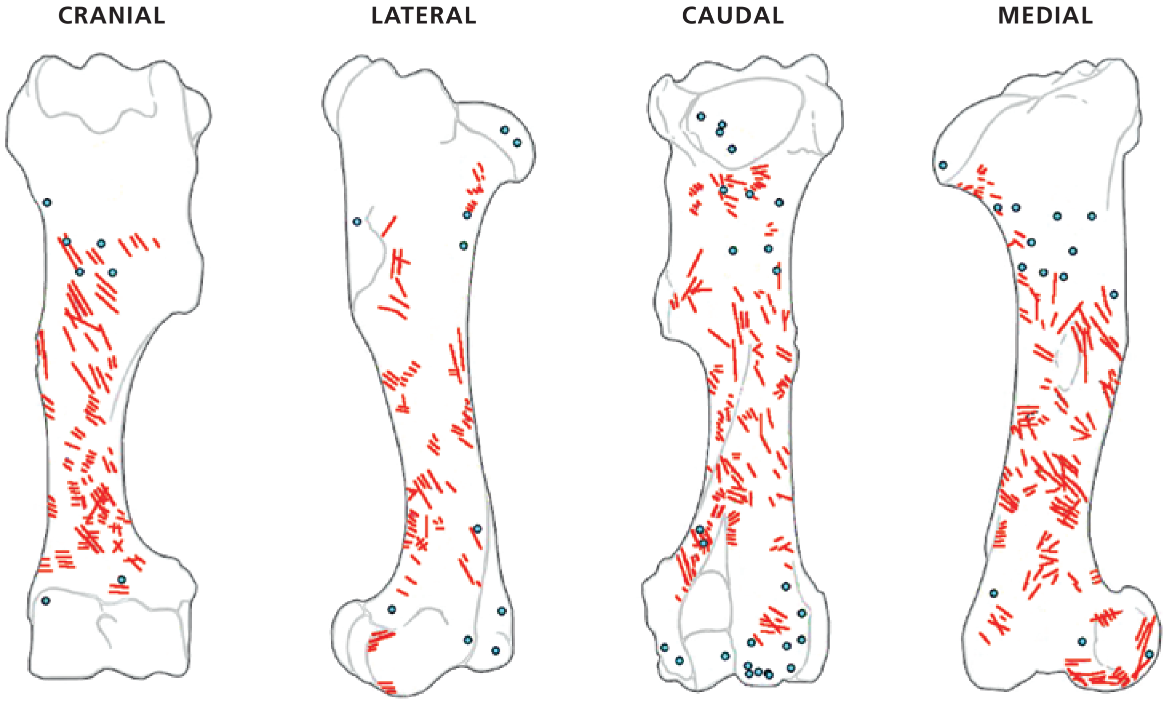


Fig. 11 Composite drawing of cut-mark (red lines) and carnivore tooth mark (cyan circles) locations on all identifiable adult horse (*Equus mosbachensis*) left humeri.

grid for the site and calculated the number of faunal remains showing butchery marks and carnivore damage appearing within each cell. In calculating the CBI, butchery marks include cut-marks, scraping marks, and impact marks; carnivore damage is wide-ranging, and includes all tooth pits, punctures, scores, furrowing, and other damage typical of carnivore feeding. These counts represent only the total number of bones with each modification and do not account for intensity of modification. Finally, the CBI was calculated for each cell of the grid: Carnivore/Butchery Index (CBI) = $(b_1 / [b_1 + c_1]) - (c_1 / [b_1 + c_1])$
where b_1 is the number of bones showing butchery marks in cell 1 and c_1 is the number of bones with carnivore damage in cell 1. Bones that included butchery marks and carnivore damage were counted once in each category. The resulting CBI ranged from 1 to -1, wherein a value of 1 indicates 100 % of the modified bones show traces of butchery and a value of -1 indicates 100 % of the modified bones show traces of carnivore damage.

RESULTS

Carnivore remains from Schöningen 13II-4

Overall, carnivore remains are rare in the Schöningen 13II-4 deposit, totalling only 25 specimens from five taxa (**Tab. 1**; **Fig. 4**), including wolf (*Canis lupus*), red fox (*Vulpes vulpes*), a large felid, possibly cave lion (cf. *Panthera leo spelaea*), badger (*Meles meles*), and a small weasel (*Mustela* sp.). Some of these specimens were originally reported by van Kolfschoten (2003, 2012, 2014; van Kolfschoten et al., 2015). Four additional remains could only be identified to large carnivore, approximately wolf-sized or larger.

		Horse				Red deer				Bison/Aurochs		
Skeletal Part		NISP	Cut	Carn		NISP	Cut	Carn		NISP	Cut	Carn
Tooth		933	-	-		59	-	-		17	-	-
Cranium		251	10	6		91	0	0		23	1	0
Hyoid		72	0	4		1	0	0		0	0	0
Mandible		487	72	12		9	0	0		13	6	0
Cervical		499	17	4		12	0	1		7	2	0
Thoracic		1,017	38	63		8	2	1		14	1	1
Rib		2,145	186	229		20	5	7		45	2	2
Sternum		3	0	0		0	0	0		0	0	0
Lumbar		317	10	11		9	0	1		4	0	0
Sacrum		66	2	3		1	0	1		3	0	0
Caudal		20	0	1		0	0	0		0	0	0
Scapula		152	8	16		8	0	2		1	0	0
Humerus		301	120	40		12	1	1		12	5	1
Radius		361	125	13		11	2	1		7	2	1
Ulna		96	16	21		7	0	1		11	0	2
Carpals		135	0	3		11	0	0		13	0	0
Metacarpal		137	27	8		13	3	1		9	2	0
Acc. metacarpal		63	3	4		-	-	-		-	-	-
Pelvis		205	28	26		12	0	4		2	0	0
Femur		351	122	30		5	1	2		20	8	1
Patella		25	0	3		2	0	1		1	0	0
Tibia		358	116	21		13	2	4		15	5	1
Fibula		7	0	0		2	0	0		4	0	0
Tarsals		173	7	15		8	1	0		18	0	0
Metatarsal		129	40	5		17	4	1		14	8	4
Acc. metatarsal		70	13	2		-	-	-		-	-	-
1st phalange		74	1	9		5	0	0		11	0	1
2nd phalange		66	0	3		6	0	0		7	0	0
3rd phalange		54	0	0		4	0	0		4	0	0
Sesamoid		81	0	0		8	0	0		13	0	0
Total		**8,648**	**961**	**552**		**354**	**21**	**29**		**288**	**42**	**14**
% NISP modified			**12.46**	**7.15**			**9.86**	**13.62**			**16.15**	**5.38**

Tab. 3 Skeletal part representation for horse (*Equus mosbachensis*), red deer (*Cervus elaphus*), and combined bison and aurochs (*Bison/Bos*) sample from Schöningen 13II-4 measured by number of identified specimens (NISP). Frequency of cut-marks (Cut) and carnivore marks (Carn) per skeletal element are tabulated by NISP and % NISP (excluding teeth).

		Horse			Red deer			Bison/Aurochs	
		Carnivore	Cut		Carnivore	Cut		Carnivore	Cut
Axial skeleton		333	335		11	7		3	12
Adult		298	291		10	6		3	10
Subadult		35	44		1	1		0	2
Appendicular skeleton		219	626		18	14		11	30
Adult		152	590		17	13		9	30
Subadult		67	36		1	1		2	0

Tab. 4 Frequency (NISP) of carnivore tooth marks and cut-marks on the axial and appendicular skeletons of the three primary ungulate taxa at Schöningen 13II-4. Data for adults and subadults are also presented individually. Some specimens may include carnivore tooth marks and cut-marks.

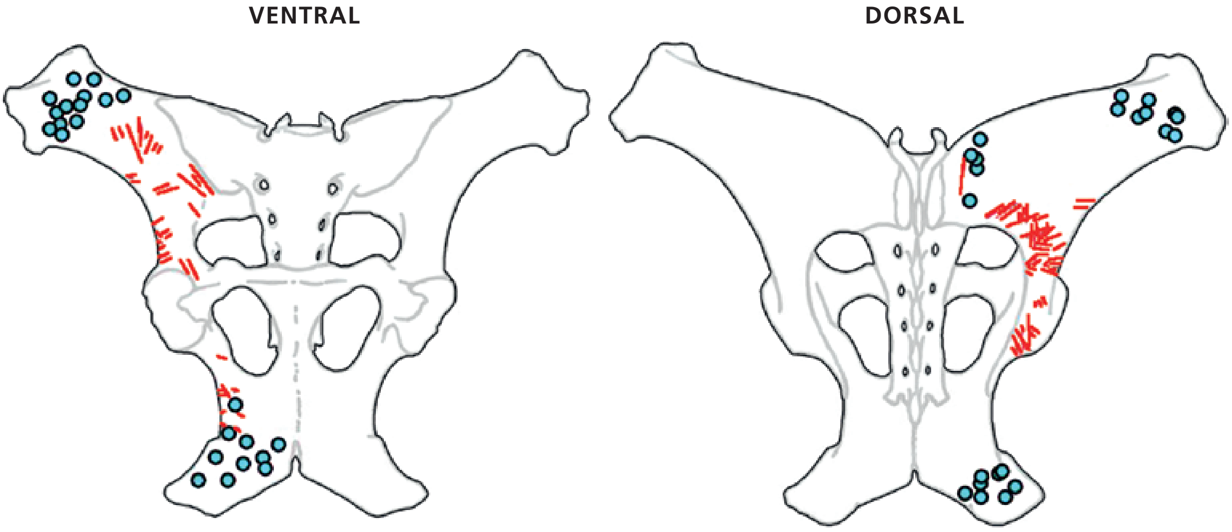


Fig. 12 Composite drawing of cut-mark (red lines) and carnivore tooth mark (cyan circles) locations on all identifiable adult horse (*Equus mosbachensis*) right innominates.

Wolf remains are the most numerous, with seven post-cranial elements (see **Tab. 1**). A minimum of two individuals is indicated by the presence of two innominates (one nearly-complete, one ilium fragment) from the right side. Based on a limited set of anatomical measurements, the Schöningen wolves appear to be of intermediate size for Pleistocene canids (**Tab. 2**). There is a well-established size gradient within the *Canis* genus in Western Europe, with increasing body size through time (Bonifay, 1971; Boudadi-Maligne, 2011; Brugal and Boudadi-Maligne, 2011). The complete radius (ID 18835; **Fig. 5**) from Schöningen is significantly longer than any example of *Canis mosbachensis* individuals from late Lower to early Middle Pleistocene sites in Germany and France. The size of the Schöningen radius closely approximates the range of *Canis lupus* remains from late Middle Pleistocene and some Upper Pleistocene contexts in France, and is substantially shorter than any more recent Upper Pleistocene individuals. The proximal femur (ID 21099) from Schöningen is also positioned in precisely the same position along the *Canis* temporal size gradient (see **Tab. 2**).

The red fox assemblage consists of a maxilla fragment, rib shaft, and distal tibia (see **Tab. 1**). The maxilla fragment preserves the canine, P1, P3, and P4, the combined morphology and dimensions of which overlap with modern *Vulpes vulpes* and Middle Pleistocene specimens from Escale and Lunel Viel (van Kolfschoten, 2003; van Kolfschoten et al., 2015).

A number of mustelid remains are present in the assemblage. The larger remains have been identified as badger, whereas the smaller skeletal material could only be identified to the genus *Mustela* (see **Tab. 1**). *Mustela erminea*, *Mustela nivalis*, and a specimen from the genus *Martes* were reported by van Kolfschoten (2012, 2014), but the material available for this study did not allow for precise taxonomic determinations.

A single bone from a large felid was identified in the Schöningen 13II-4 assemblage (see **Tab. 1**). The thoracic vertebra (**Fig. 6**) was submitted for zooarchaeology by mass spectroscopy (ZooMS) analysis and returned a signature consistent with cave lion (*Panthera leo spelaea*) (Frido Welker, personal communication, publication forthcoming). It should be noted that sabre-toothed cat (*Homotherium latidens*) has been reported from the Schöningen 13II-4 main excavation and from the nearby Obere Berme (Serangeli et al., 2015; Janssens et al., 2019). These remains were excavated after 2008 and are not directly associated with the Schöningen 13II-4 main excavation and are thus not part of the current study. Only postcranial remains of saber-toothed cat, which may not be readily distinguished from cave lion (Diedrich and McFarlane, 2017),

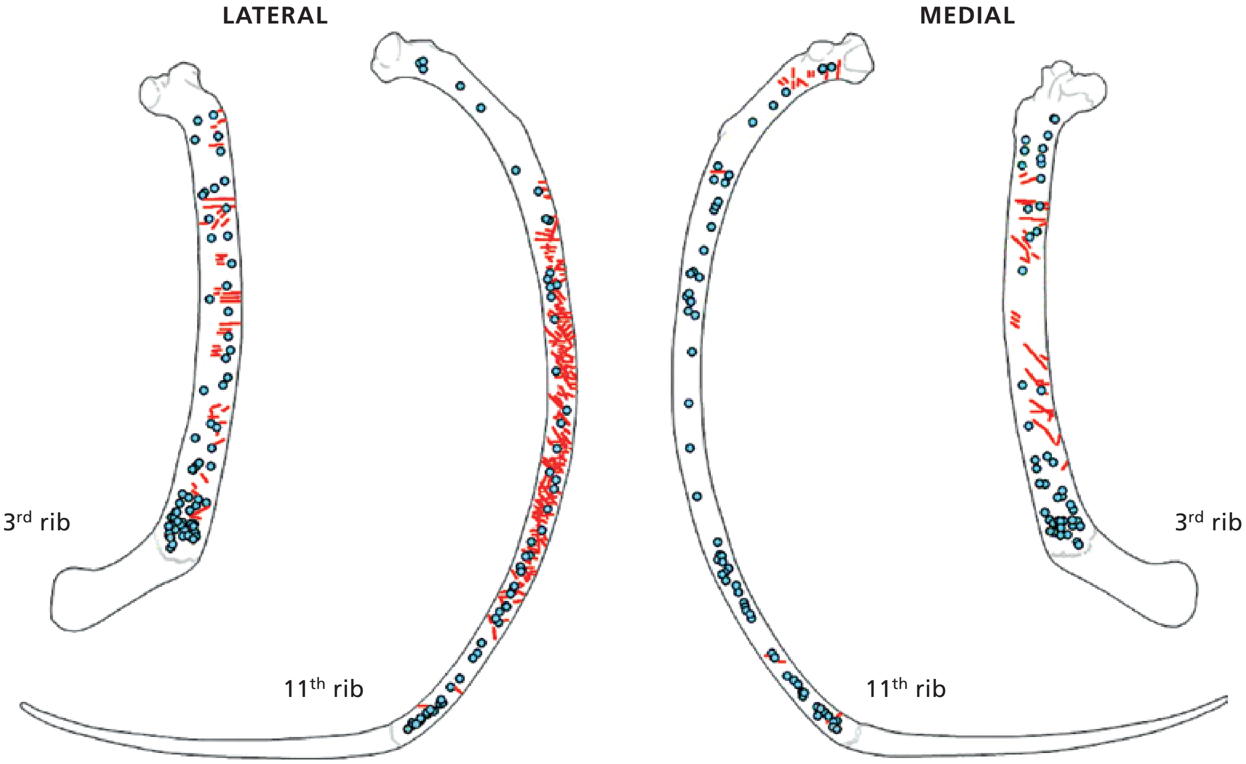


Fig. 13 Composite drawing of cut-mark (red lines) and carnivore tooth mark (cyan circles) locations on all identifiable adult horse (*Equus mosbachensis*) left ribs. '3rd rib' represents composite of ribs 1-6; '11th rib' represents composite of ribs 7-18.

originated from the Schöningen 13II-4 main excavation area; however, isolated saber-toothed cat dental material has been discovered within the Obere Berme deposit.

Three additional rib shaft fragments and a possible coprolite fragment were identified as large carnivore (see **Tab. 1**), wolf-sized or larger.

Carnivore remains at Schöningen 13II-4 are spatially dispersed (see **Fig. 4**), with no remains from a single species clustered together. The overall faunal assemblage is heavily concentrated along a narrow strip oriented north-south in the central portion of the site, which likely corresponds to the shoreline of the lake during a period of increased hominin activity. A number of carnivore remains were recovered within or near this central concentration, most in the northern portion of the site and few in the south. A smaller number of carnivore remains were recovered from the eastern portion of the site, likely corresponding to additional shorelines during times of lowered lake levels and reduced hominin activity (Turner et al., 2018; García-Moreno et al., 2021).

Traces of carnivores at Schöningen 13II-4

Whereas carnivore remains are relatively rare at Schöningen 13II-4, damage to ungulate bones in the form of carnivore tooth pits, punctures, scores, and the like (**Figs. 7-10**) is abundant. Across the three primary ungulate taxa (horse, red deer, bison/aurochs) a total of 595 remains (NISP) preserve carnivore damage (**Tab. 3**). In contrast, 1,024 of those remains show cut-marks. In the horse assemblage, cut-marks are substantially more abundant than carnivore damage on the meat-bearing bones of the appendicular skeleton

(**Tab. 4**), particularly the long bones, scapula, and innominate. On the other hand, cut-marks and carnivore damage are equally distributed on the axial skeleton, mostly ribs and vertebrae. A closer look at carnivore damage and cut-marks across the axial and appendicular skeletons reveals differences in the treatment of adult and juvenile carcasses (see **Tab. 4**). Carnivore marks slightly outnumber cut-marks (298 : 291) on adult axial skeletal parts; for the juvenile axial skeleton, the ratio of carnivore-damaged-to-cut-marked bones is 35 : 44. There is no significant difference between the frequencies of carnivore marks and cut-marks on adult and juvenile bones when considering the axial skeleton ($\chi^2 = 1.10$, $p = 0.29$). On adult appendicular remains there are far fewer carnivore marks than cut-marks (152 : 590); for juveniles, carnivore damage is nearly twice as frequent as cut-marks (67 : 36). This sharp contrast is statistically significant ($\chi^2 = 93.55$, $p < 0.00001$), suggesting that hominins processed the carcasses of adult and juvenile horses differently, thus leaving different portions of adult and juvenile horse carcasses to be scavenged by carnivores.

For the much smaller red deer assemblage, carnivore damage occurs more frequently than cut-marks on all portions of the skeleton (see **Tab. 3-4**). A higher frequency of carnivore-modified bones may indicate increased competition among scavengers for access to red deer carcasses abandoned by hominins. The opposite pattern is observed in the combined bison and aurochs assemblage, with cut-marks outnumbering carnivore damage on axial and appendicular skeletons. Overall, carnivore involvement with the bison/aurochs assemblage was minimal. There are too few juvenile red deer and bison/aurochs remains to determine if hominins treated the carcasses of adults and subadults differently.

The locations of cut-marks and carnivore tooth marks on horse bones are clearly differentiated. For long bones, cut-marks are concentrated on the mid-shafts, showing intensive filleting of meat from the bones. **Figure 11** shows this general trend in the humeri, which is replicated across most of the long bone elements. Fewer cut-marks are preserved toward the epiphyses, corresponding to disarticulation of long bones at the joints. It should be noted, however, that long bone shafts preserved more frequently than epiphyses, in general. In contrast to cut-mark locations, carnivore tooth marks occur at or near the epiphyses and are almost never found on mid-shafts. This is a well-recognized pattern among large carnivores, wherein defleshed bones are gnawed from the epiphyses and down the mid-shaft (e. g., Haynes, 1980, 1982, 1983), sometimes

Fig. 14 Cut-marks beneath carnivore tooth puncture on horse (*Equus mosbachensis*) left ilium (ID #11820).

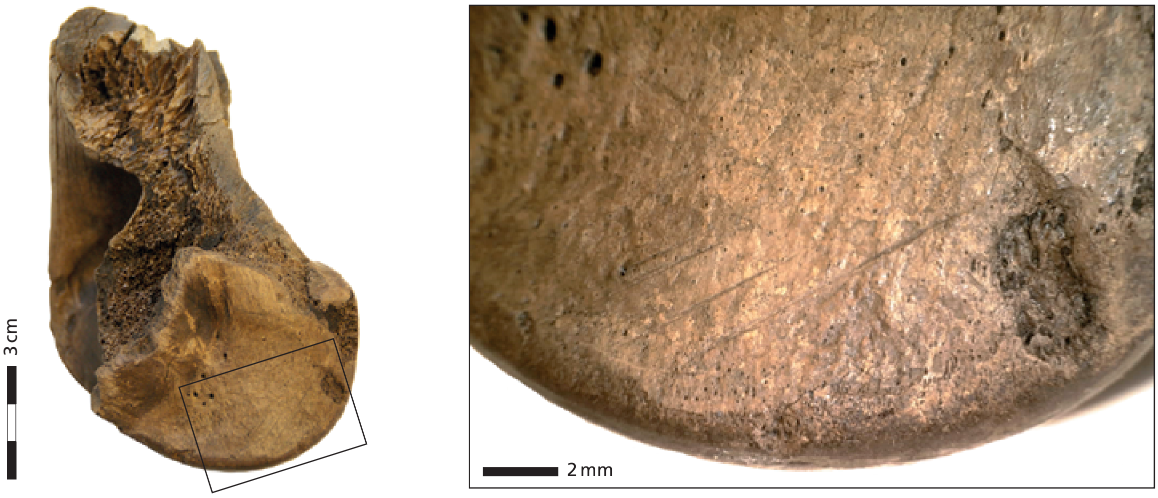


Fig. 15 Cut-marks beneath carnivore tooth pit on horse (*Equus mosbachensis*) left humerus (ID #5031).

resulting in long bone cylinders (see **Fig. 10**). The complete consumption of long bone epiphyses and other bone portions, which is common in the Schöningen assemblage, is a pattern more prevalent among hyena and canids rather than felids (Domínguez-Rodrigo et al., 2012). On innominates, cut-marks occur near the acetabulum and adjacent portions of the ilium and ischium (**Fig. 12**). The positions of these cut-marks relate to filleting and dismembering. There is little overlap with the locations of carnivore marks, which are mostly restricted to the prominent and easily accessible portions at the crest of the ilium and ischial tuberosity. Cut-marks on ribs are concentrated on the central portion of the rib shaft, whereas carnivore marks appear most frequently at the distal ends (**Fig. 13**). Often carnivores consumed some portion of the distal end of the rib, leaving tooth pits, punctures, and scores further toward the proximal ends of rib shafts; this is the likely cause of the carnivore damage to the shaft portions of the ribs depicted in **Figure 13**. Overall, it seems that gnawing from the proximal ends of ribs was less frequent that gnawing from the distal ends.

Carnivore tooth marks and cut-marks are far less frequent on red deer and bison/aurochs bones, but follow the same general pattern as observed in the horse assemblage.

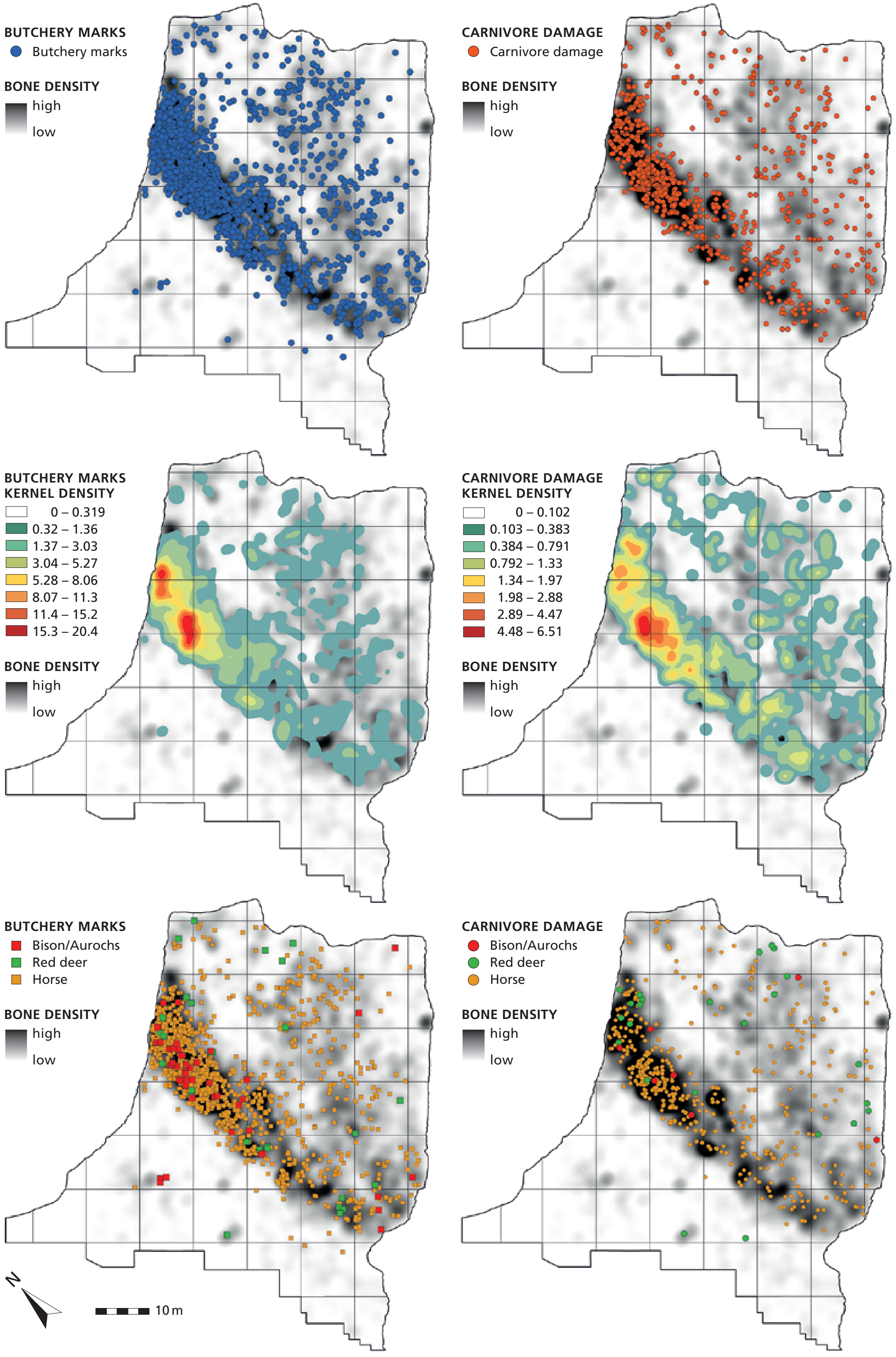
In terms of overall frequency and placement of carnivore marks and cut-marks, all evidence indicates that carnivore damage to bones was secondary to hominin butchery. This sequence has been confirmed by an in-depth study on the relative timing of various markings on a sample of the most heavily-modified remains (Lehnig et al., 2021). Furthermore, nine bones preserve overlapping carnivore damage and cut-marks, and in all cases the cut-marks occur beneath the carnivore tooth damage (**Figs. 14-15**).

Spatial distribution of carnivore traces at Schöningen 13II-4

Faunal remains at Schöningen 13II-4 are concentrated along a narrow strip extending in a north-south direction across the central portion of the site. Bones with traces of carnivore activity and hominin activity (cut-marks, impact marks, scraping marks) mirror this overall pattern (**Fig. 16**), especially in the northernmost

→

Fig. 16 Overall distribution of faunal remains showing butchery marks (cut-marks, impact marks, and scrapping marks) (right) and carnivore damage (left), including Kernel density analysis (centre) and distribution by taxa (lower).


BUTCHERY MARKS
● Butchery marks
BONE DENSITY
high
low
CARNIVORE DAMAGE
● Carnivore damage
BONE DENSITY
high
low
BUTCHERY MARKS KERNEL DENSITY
0 – 0.319
0.32 – 1.36
1.37 – 3.03
3.04 – 5.27
5.28 – 8.06
8.07 – 11.3
11.4 – 15.2
15.3 – 20.4
BONE DENSITY
high
low
CARNIVORE DAMAGE KERNEL DENSITY
0 – 0.102
0.103 – 0.383
0.384 – 0.791
0.792 – 1.33
1.34 – 1.97
1.98 – 2.88
2.89 – 4.47
4.48 – 6.51
BONE DENSITY
high
low
BUTCHERY MARKS
■ Bison/Aurochs
■ Red deer
■ Horse
BONE DENSITY
high
low
CARNIVORE DAMAGE
● Bison/Aurochs
● Red deer
● Horse
BONE DENSITY
high
low
N
10 m

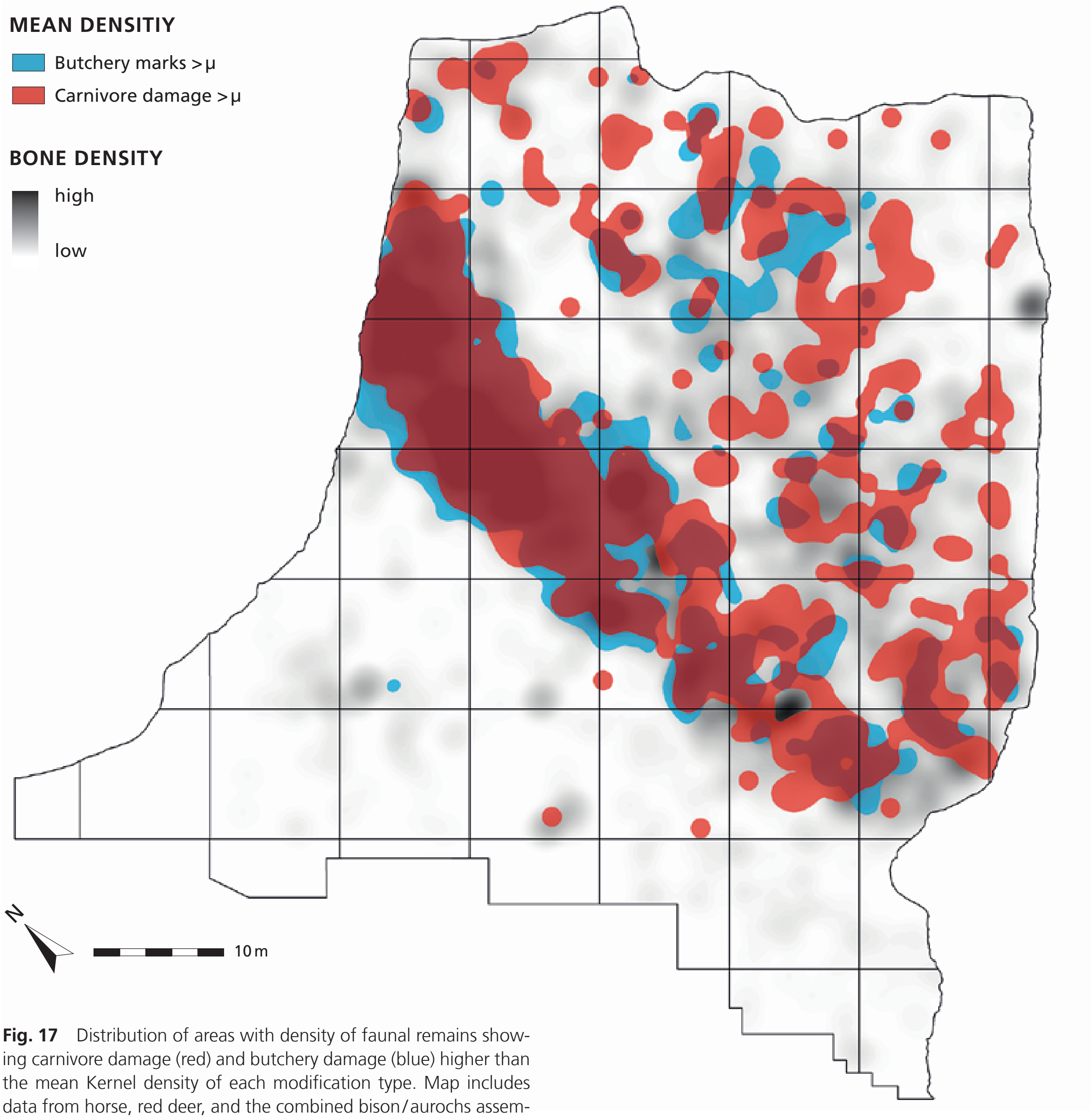


Fig. 17 Distribution of areas with density of faunal remains showing carnivore damage (red) and butchery damage (blue) higher than the mean Kernel density of each modification type. Map includes data from horse, red deer, and the combined bison/aurochs assemblage.

portion of the site where the densest concentration of bones were recovered. Fewer bones impacted by carnivores and hominins were found to the east of the main concentration and almost none were recovered to the west. Bones with carnivore damage are more dispersed than bones showing butchery marks (average distance: 0.72 m *vs*. 0.37 m) (see **Fig. 16**). For horse and the combined bison and aurochs samples, most of the modified bones occur within the main concentration. For the red deer, hominin-modified and carnivore-damaged bones are nearly as frequent in the eastern portion of the site as in the main concentration (see **Fig. 16**); this pattern mimics the distribution of red deer bones in the entire assemblage.

Figure 17 shows the areas where the density of faunal remains showing carnivore damage and butchery marks is higher than the estimated Kernel mean density for each type of bone surface modification. Carni-

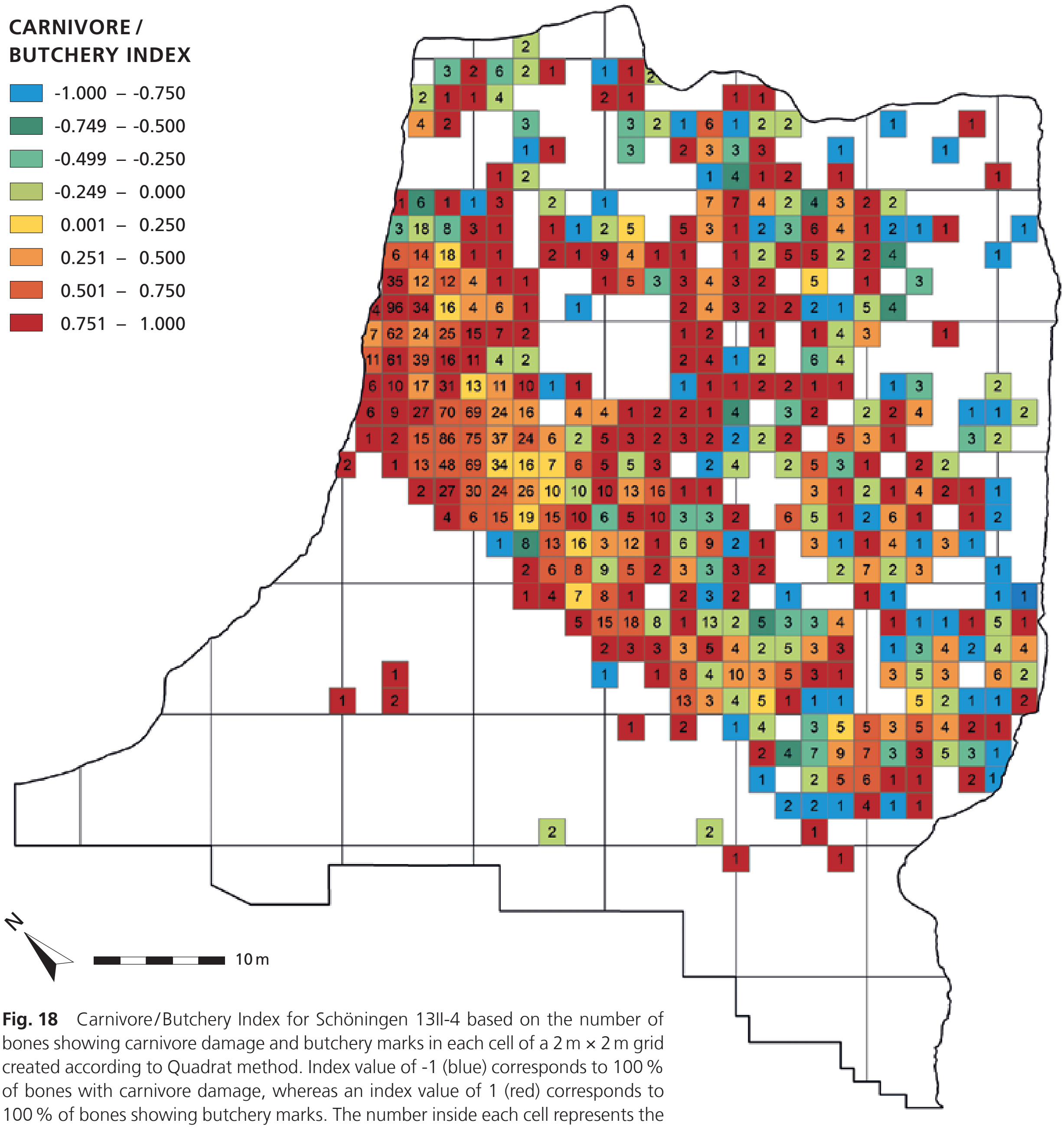


Fig. 18 Carnivore/Butchery Index for Schöningen 13II-4 based on the number of bones showing carnivore damage and butchery marks in each cell of a 2 m × 2 m grid created according to Quadrat method. Index value of -1 (blue) corresponds to 100 % of bones with carnivore damage, whereas an index value of 1 (red) corresponds to 100 % of bones showing butchery marks. The number inside each cell represents the total number of modified faunal remains in it.

vore damage and butchery marks overlap quite neatly within the main concentration, especially within the northern half. In contrast, the picture in the eastern portion of the site is different, with smaller patches of carnivore-damaged bones and hominin-modified bones barely overlapping. However, this difference may be a consequence of the different overall spatial patterning, since finds are less abundant and more scattered in the eastern portion of the site.

The CBI shows that butchery marks are clearly dominant in the northern part of the main concentration (**Fig. 18**), where the larger and densest clusters of faunal remains are located. In contrast, the southern part of the main concentration shows a patchier distribution, where cells containing bones with butchery marks alternate with cells with bone showing carnivore damage; however, the number of modified remains

Taxa		Europe 400-200 ka[1]	Europe 200-0 ka[1]	Bilzingsleben[2]	Schöningen 12II-1[3]	Schöningen 12B[4]	Schöningen 13II-2[4]	Schöningen 13II-3[4]	**Schöningen 13II-4[5]**	Schöningen Obere Berme[6]	Weimar-Ehringsdorf[7]	Neumark Nord 1 & 2[8]	Salzgitter-Lebenstedt[9]
Hyenids	*Pliocrocuta perrieri*		?										
	Crocuta crocuta	+	+	+							+	+	
	Hyaena prisca	+											
Canids	*Canis lupus*	+	+	+			+		**+**		+	+	+
	Cuon priscus	+											
	Cuon alpinus		+										
	Vulpes vulpes	+	+	+					**+**		+	+	
	Alopex lagopus		+										
Felids	*Panthera leo spelaea*	+	+	+	+	+			**+**		+	+	
	Homotherium latidens		?							+			
	Large felid											+	
	Lynx pardina / spelaea	+	+										
	Lynx lynx		+								+		
	Felis lunensis / silvestris	+	+	+									
Ursids	*Ursus arctos*	+	+								+		
	Ursus spelaeus	+	+			+					+		
	Ursus thibetanus	+	+			+					+		
	Ursus sp.			+	+						+	+	
Mustelids	*Meles meles*	+	+	+	+				**+**		+		
	Gulo gulo		+										
	Martes sp.		+	+				+			+		
	Mustela sp.	+	+					+	**+**		+		
	Lutra lutra	+	+	+							+*		

Tab. 5 Carnivore species present in late Middle Pleistocene Western and Central Europe, several Schöningen localities, and other key German sites. Archaeological sites are ordered approximately from oldest to youngest, left to right.

[1] Croiter and Brugal, 2010
[2] Müller and Pasda, 2011; all fauna from 1969-2003 excavations
[3] Julien et al., 2015a
[4] van Kolfschoten, 2014
[5] Hutson et al., 2020, and this study
[6] Starkovich and Conard, 2015
[7] Schäfer et al., 2007; all levels
[8] Kindler et al., 2020; all levels
[9] Gaudzinski, 1999
+* *Cyrnaonyx antiqua* – Pleistocene otter

per cell is substantially lower than in the northern portion of the site. Cells containing bones with more carnivore damage occur along the edges of the main concentration, but the overall density of butchered bones in the main concentration is simply too high to discern any clear pattern in the spatial distribution of carnivore damage. These results suggest that carnivore activity can be better tracked in the eastern half of the site where the faunal remains are less abundant and more scattered. Here, cells containing bones with carnivore damage often appear at the periphery of cell clusters showing butchery. This pattern could indicate that portions of previously butchered animal carcasses were slightly displaced during scavenging events by one or more carnivores.

Which carnivores were active at Schöningen 13II-4?

Based on the evidence presented here, our assessment on the role of carnivores in the formation of the Schöningen 13II-4 deposit is that of scavengers. The carnivore remains themselves provide the most direct evidence for which carnivores species may have scavenged from the hominin kills along the Schöningen lakeshore (see **Tab. 1**). Because of the substantial carnivore damage to many of the bones, the largest species, namely wolf and lion, are potential scavenger candidates, but fox and badger cannot be discounted entirely. We also cannot restrict the range of potential scavenging carnivores to only those represented in the Schöningen 13II-4 assemblage. Other carnivore species were undoubtedly present on the landscape, but either none died at the small stretch of shoreline represented in Schöningen 13II-4 deposit or their bones did not preserve. Schöningen 13II-4 includes the richest carnivore assemblage of all the well-studied Schöningen sites, but contains relatively few carnivore species compared to all carnivores present in Pleistocene Europe from 400 ka onward (**Tab. 5**). Additional Schöningen localities and regional interglacial sites shed further light on the possible presence of different carnivore species on the landscape. Hyenids are absent from all Schöningen localities, but spotted hyena (*Crocuta crocuta*) does appear in the post-Elsterian (i. e., post-MIS 12) travertine deposits from Bilzingsleben, as well as at the interglacial sites of Weimar-Ehringsdorf (MIS 7) and Neumark-Nord (MIS 5e). Of the several canid species present in Europe during the late Middle Pleistocene, wolf (*Canis lupus*) and red fox (*Vulpes vulpes*) appear most consistently, including at Schöningen 13II-4. Lion (*Panthera leo spelaea*) is nearly as ubiquitous as wolf, persisting in Europe into the Late Pleistocene; ZooMS analysis confirms its presence at Schöningen 13II-4. The presence of sabre-toothed cat (*Homotherium latidens*) in main excavation at Schöningen 13II-4 is problematic and does not appear in any other post-Elsterian sites in the region. Smaller felids, such as the lynx (*Lynx lynx*) and wildcat (*Felis sylvestris*) were present but probably rare in open lakeshore habitats such as Schöningen, but lynx is present at Weimar-Ehringsdorf. Schöningen 13II-4 preserved no ursid remains, but cave bear (*Ursus spelaeus*) and Asian black bear (*Ursus thibetanus*) have been identified at Schöningen 12B from a level that likely corresponds to the peak of the locally-defined Reinsdorf Interglacial (Urban and Sierralta, 2012); however, the Asian black bear is primarily herbivorous and the isotopic composition of cave bear remains reveals a predominant herbivore signature (Bocherens, 2019). Ursid remains are also found at Bilzingsleben and Weimar-Ehringsdorf, including brown bear (*Ursus arctos*), which was likely more carnivorous than cave bear and Asian black bear. A variety of mustelid species are present at several Schöningen localities, including Schöningen 13II-4, and must have been frequent visitors to the Schöningen lakeshore, but were not likely to have been significant affecters of the Schöningen 13II-4 faunal assemblage. In reviewing the regional carnivore record, hyena and bear should be added to wolf and lion as potential scavengers of hominin kills at Schöningen 13II-4.

To narrow this list of possible scavenging carnivores, we look to traces of carnivore damage on the Schöningen bones, i. e., tooth pits and tooth scores, to determine if there is any measurable overlap with pit and score dimensions from modern carnivores. Mean pit length in the Schöningen sample is larger than any of the carnivore samples (**Tab. 6**; **Fig. 19**), falling closest to the pooled lion sample, but this is not statistically significant. For mean pit breadth, the Schöningen sample is again measurably larger than all of the pooled carnivore samples, except for lion (**Tab. 7**; **Fig. 20**); the difference between mean pit breadth for the Schöningen and pooled lion samples is not statistically significant. In terms of mean score length, the Schöningen sample shows statistical similarities with wolf, mountain lion, and bear (**Tab. 8**; **Fig. 21**). Finally, mean pit breadth at Schöningen is statistically similar to the bear sample (**Tab. 9**; **Fig. 22**).

In all respects, the dimensions of carnivore tooth pits and scores from the Schöningen sample are very large. Only the largest carnivores – wolf, lion, hyena, bear – could have made these marks on the Schöningen bones.

	Pit length [mm]					
Reference	N	Mean	Min	Max	SD	95 % CI
Fox						
Andrés et al., 2012	108	1.93	0.36	9.07	1.40	1.66-2.19
Delaney-Rivera et al., 2009	8	1.09	0.43	2.91	0.81	0.53-1.66
Young et al., 2014	442	1.66	0.15	6.10	0.96	1.57-1.75
Total fox	558	1.71	0.15	9.07	1.06	1.62-1.79
Dog						
Andrés et al., 2012	85	1.91	0.50	9.88	0.99	1.70-2.12
Delaney-Rivera et al., 2009	45	1.37	0.65	4.21	0.68	1.30-1.44
Young et al., 2014	15	3.11	1.97	4.81	0.97	2.62-3.60
Total dog	145	1.87	0.50	9.88	1.03	1.70-2.03
Coyote						
Delaney-Rivera et al., 2009	17	2.17	0.66	5.19	1.17	1.61-2.73
Jackal						
Domínguez-Rodrigo and Piqueras, 2003	80	2.48	-	-	1.26	-
Wolf						
Sala et al., 2014	512	2.85	0.76	7.41	1.16	2.75-2.95
Andrés et al., 2012	365	2.89	0.40	9.95	1.44	2.74-3.03
Campmas and Beauval, 2008	2,238	2.32	0.14	14.24	1.74	2.25-2.39
Wolfspark Kasteelberg, this study	249	6.58	1.49	22.48	3.14	6.19-6.97
Total wolf	3,364	2.78	0.14	22.48	2.10	2.71-2.85
Hyena						
Andrés et al., 2012	779	1.99	0.17	25.60	1.73	1.87-2.12
Delaney-Rivera et al., 2009	8	2.83	1.35	5.35	1.64	1.69-3.96
Sala, 2012	167	3.29	0.80	20.00	2.52	2.91-3.68
Total hyena	954	2.23	0.17	25.60	1.95	2.10-2.35
Bobcat						
Delaney-Rivera et al., 2009	75	1.84	0.35	5.72	1.16	1.58-2.10
Mountain lion						
Delaney-Rivera et al., 2009	86	2.05	0.41	5.96	1.36	1.76-2.33
Lion						
Andrés et al., 2012	206	5.72	0.98	23.30	3.51	5.24-6.20
Delaney-Rivera et al., 2009	47	2.24	0.78	8.16	1.69	1.76-2.72
Sala, 2012	190	4.79	1.77	10.18	1.85	4.53-5.06
Total lion	443	5.03	0.78	23.30	3.26	4.72-5.33
Bear						
Saladié et al., 2013	285	3.46	0.50	9.86	1.88	3.24-3.68
Domínguez-Rodrigo and Piqueras, 2003	58	4.68			2.70	3.98-5.37
Sala, 2012	36	4.90	2.36	10.13	1.74	4.33-5.47
Total bear	379	3.78	0.50	10.13	2.09	3.57-3.99
Schöningen, this study	186	5.68	1.56	25.89	3.29	5.21-6.15

Tab. 6 Reference data for carnivore tooth pit lengths (mm): sample size (N), mean, minimum (Min), maximum (Max), standard deviation (SD), 95 % confidence intervals (95 % CI). Dataset includes punctures if provided in original source.

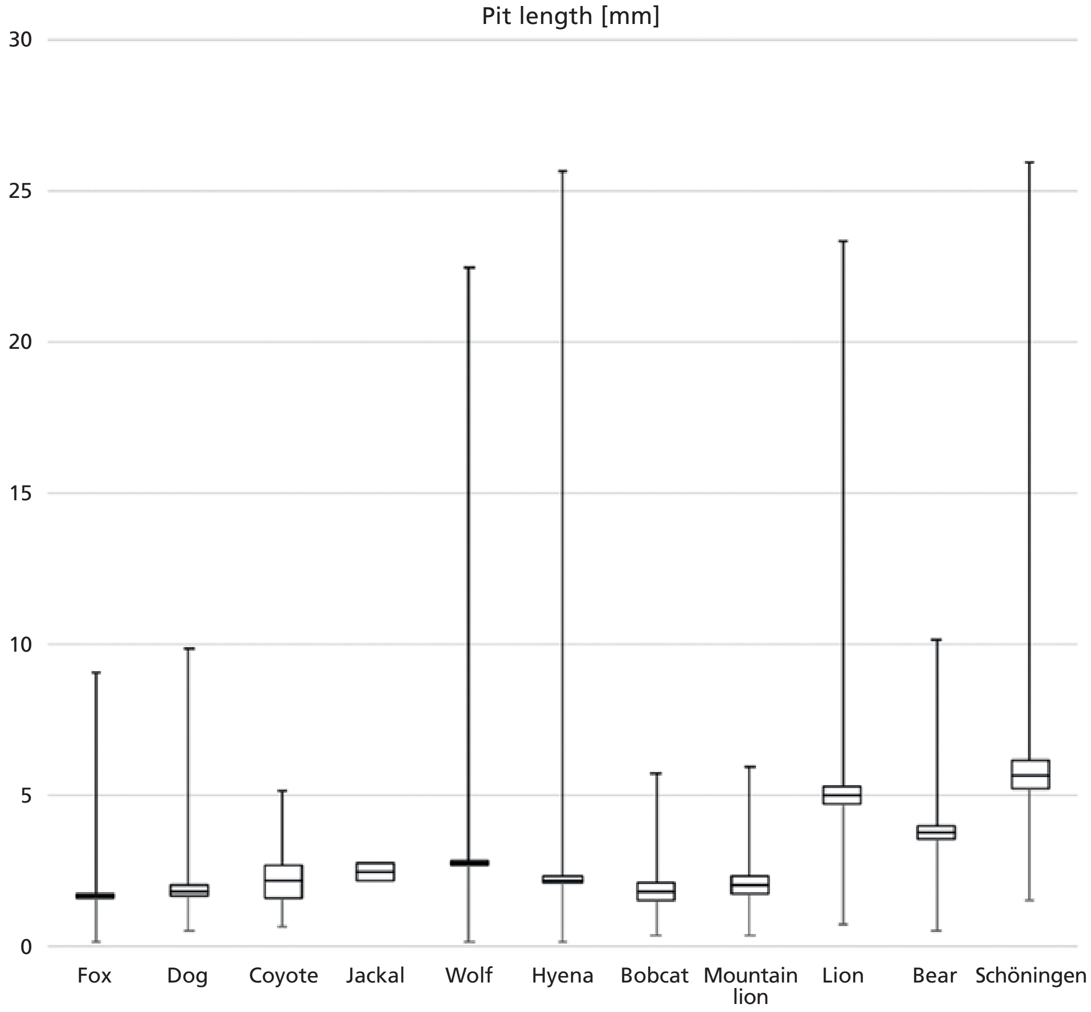


Fig. 19 Comparison of tooth pit lengths among several carnivore species and the Schöningen sample. Data represent median pit length with 95 % confidence intervals and minimum and maximum values from **Tab. 6.**

The hyena's reputation as a bone crunching carnivore is well deserved, but the individual marks imparted on bones by hyenas are quite small relative to other carnivores, and even sometimes superseded by smaller canid species. Considering the marks on the Schöningen sample are so large and their absence in all Schöningen faunal assemblages, hyenas likely did not scavenge from the animal carcasses abandoned by hominins at the Schöningen lakeshore.

Even the dimensions of pits made by wolves are much smaller than those recorded in the Schöningen sample, although score lengths are similar between the two datasets. Interestingly, dimensional data for the *Adler- und Wolfspark* Kasteelburg sample reported here is also quite high relative to other carnivores, even much higher than other wolf samples, and more closely approximates the sample from Schöningen 13II-4. This loose affinity with tooth mark dimensions supports the suggestion that wolves likely played a prominent role in scavenging at Schöningen 13II-4, which is also underscored by the presence of at least two wolf individuals in the Schöningen 13II-4 faunal assemblage. Voormolen (2008) and van Kolfschoten et al. (2015) also suggest the gnawing damage at Schöningen 13II-4 was inflicted by wolves, both citing the placement and intensity of damage observed by Haynes (1983).

	Pit breadth [mm]					
Reference	N	Mean	Min	Max	SD	95 % CI
Fox						
Andrés et al., 2012	108	1.33	0.19	5.91	1.04	1.13-1.52
Delaney-Rivera et al., 2009	8	0.78	0.32	1.80	0.54	0.40-1.15
Young et al., 2014	442	1.07	0.29	4.65	0.59	1.02-1.13
Yravedra et al., 2019	41	0.45	0.13	0.75	0.18	0.40-0.51
Total fox	599	1.07	0.13	5.91	0.70	1.02-1.13
Dog						
Andrés et al., 2012	85	1.48	0.50	7.93	0.72	1.33-1.63
Delaney-Rivera et al., 2009	45	0.86	0.39	1.42	0.27	0.78-0.93
Young et al., 2014	15	2.03	1.17	4.18	0.72	1.66-2.40
Yravedra et al., 2019	34	1.62	0.31	3.32	0.70	1.38-1.85
Total dog	179	1.40	0.39	7.93	0.71	1.29-1.50
Coyote						
Delaney-Rivera et al., 2009	17	1.48	0.43	3.51	0.84	1.08-1.88
Jackal						
Domínguez-Rodrigo and Piqueras, 2003	80	2.20	-	-	1.45	-
Wolf						
Sala et al., 2014	362	2.22	0.66	6.12	0.95	2.12-2.32
Andrés et al., 2012	365	2.12	0.16	7.48	1.11	2.01-2.23
Yravedra et al., 2019	28	3.37	1.99	4.86	0.80	3.07-3.66
Wolfspark Kasteelberg, this study	249	3.01	1.28	10.96	1.27	2.85-3.16
Total wolf	1,004	2.41	0.16	10.96	1.16	3.15-3.58
Hyena						
Andrés et al., 2012	779	1.40	0.11	14.00	1.08	1.32-1.47
Delaney-Rivera et al., 2009	8	1.50	0.70	2.07	0.50	1.15-1.84
Sala, 2012	7	5.50	3.00	10.00	2.29	3.80-7.20
Total hyena	794	1.44	0.11	14.00	1.16	1.36-1.52
Bobcat						
Delaney-Rivera et al., 2009	75	1.26	0.28	4.59	0.79	1.08-1.44
Mountain lion						
Delaney-Rivera et al., 2009	86	1.48	0.33	4.93	0.98	1.28-1.69
Lion						
Andrés et al., 2012	206	3.73	0.60	15.00	2.40	3.40-4.06
Delaney-Rivera et al., 2009	47	1.43	0.46	6.32	1.16	1.10-1.76
Sala, 2012	190	3.57	1.07	9.13	1.64	3.34-3.81
Total lion	443	3.42	0.46	15.00	2.11	3.22-3.62
Bear						
Saladié et al., 2013	285	2.31	0.12	7.38	1.39	2.15-2.47
Domínguez-Rodrigo and Piqueras, 2003	58	3.28	-	-	2.01	-
Sala, 2012	36	2.84	1.64	5.85	1.45	2.37-3.32
Total bear	379	2.51	0.12	7.38	1.54	2.36-2.67
Schöningen, this study	186	3.36	0.77	8.95	1.48	3.15-3.58

Tab. 7 Reference data for carnivore tooth pit breadths (mm): sample size (N), mean, minimum (Min), maximum (Max), standard deviation (SD), 95 % confidence intervals (95 % CI). Dataset includes punctures if provided in original source.

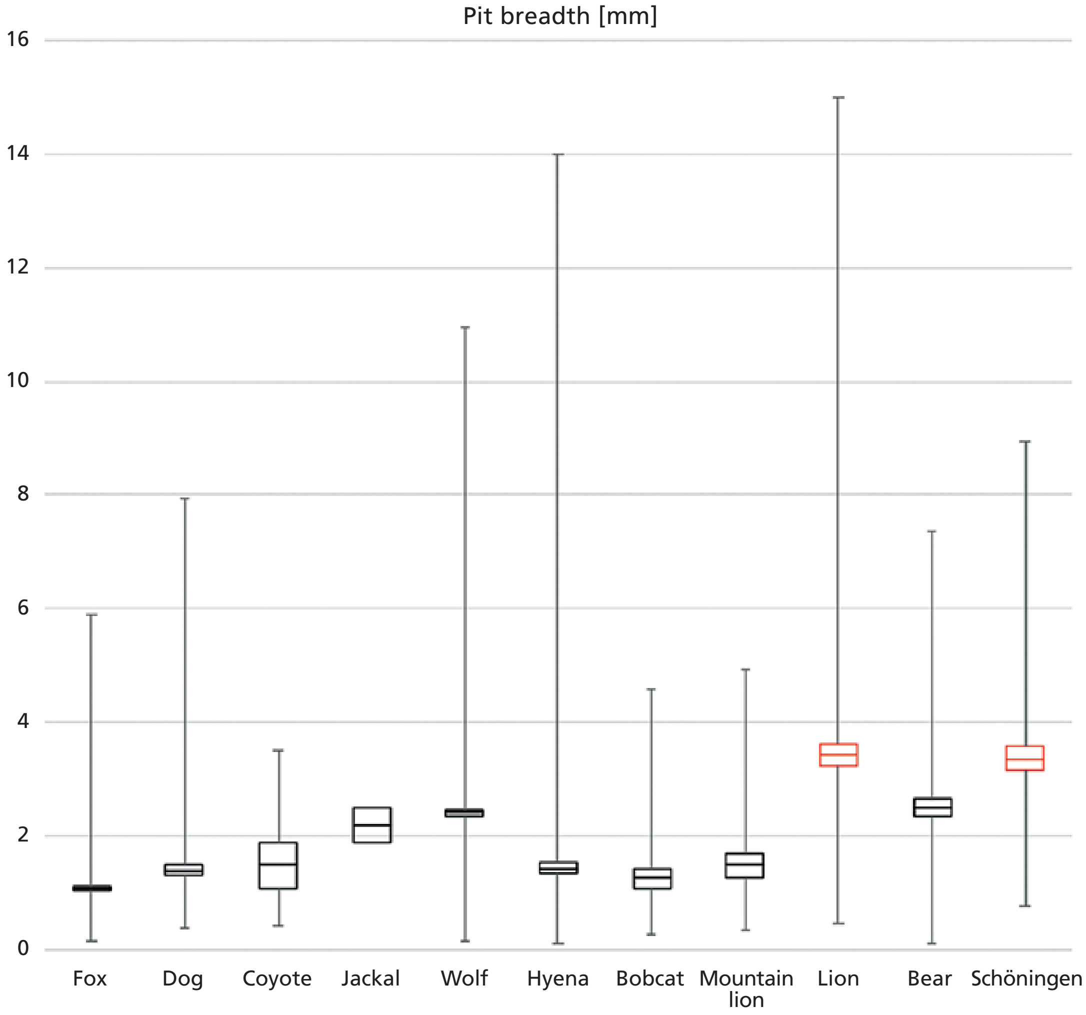


Fig. 20 Comparison of tooth pit breadths among several carnivore species and the Schöningen sample. Data represent median pit breadth with 95 % confidence intervals and minimum and maximum values from **Tab. 7.** Samples highlighted in red are not significantly different ($p \geq 0.05$) according to unpaired t-test.

Likewise, the presence of lion and some overlap with large felid tooth markings implicates lion as a potential scavenger at Schöningen 13II-4. Starkovich and Conard (2015) implicate wolf and a large felid in the modification of the Schöningen Obere Berme assemblage based on tooth pit dimensions. They identify sabre-toothed cat rather than lion as the large felid species. For Schöningen 13II-4, we argue for lion as the scavenger species due to its presence in the 13II-4 faunal assemblage, whereas the association of sabre-toothed cat with the Schöningen 13II-4 main excavation is less secure. Furthermore, Marean and Ehrhardt (1995) report that although tooth marks are common for *Homotherium*-gnawed bones, crushing and breakage is rare, features that are common in the Schöningen 13II-4 assemblage. Nevertheless, the presence of sabre-tooth cat is an intriguing possibility as Hemmer (2001) has suggested that *Homotherium* was at least partially reliant on scavenging.

Although not present in the faunal assemblage, the Schöningen sample shows similarities with bear, overlapping in score length and breadth. The ursid species identified at Schöningen 12B, cave bear and Asian black bear, are mostly herbivorous and unlikely primary modifiers of the Schöningen 13II-4 assemblage. However, supposed cave bear-scavenged bones from the Late Pleistocene site of Coro Tracito, Spain (Rabal-

Garcés et al., 2012), do show some dimensional similarities with the Schöningen sample, with a very large mean pit breadth of 5.32 mm (Schöningen: 5.68 mm) and a score breadth rarely exceeding 2.5 mm (Schöningen: 2.14 mm). Several bear species, including brown bear, are noted in the Lower Travertine at Weimar-Ehringsdorf, though the Lower Travertine fauna at Weimar-Ehringsdorf is younger than the Schöningen 13II-4 fauna by at least 70,000 years based on current age estimates. Nevertheless, it is possible that some large ursid species was actively scavenging the animal carcasses from Schöningen 13II-4.

	Score length [mm]					
Reference	N	Mean	Min	Max	SD	95 % CI
Fox						
Andrés et al., 2012	103	3.64	1.36	14.22	2.05	3.25- 4.04
Delaney-Rivera et al., 2009	2	3.28	2.87	3.69	0.58	2.48- 4.09
Young et al., 2014	90	6.89	1.94	14.09	3.12	6.25- 7.54
Total fox	195	5.14	1.36	14.22	3.05	4.71- 5.57
Dog						
Andrés et al., 2012	209	5.25	1.14	26.55	2.81	4.87- 5.63
Delaney-Rivera et al., 2009	18	4.74	2.06	9.97	1.66	3.98- 5.51
Young et al., 2014	25	9.29	2.67	18.19	4.21	7.64-10.94
Total dog	252	5.62	1.14	26.55	3.15	5.23- 6.00
Coyote						
Delaney-Rivera et al., 2009	1	3.78	-	-	-	-
Jackal						
Domínguez-Rodrigo and Piqueras, 2003	40	3.35	-	-	1.09	-
Wolf						
Andrés et al., 2012	384	9.05	1.00	32.03	4.53	8.60- 9.51
Wolfspark Kasteelberg, this study	1,067	12.83	3.96	42.46	5.40	12.50-13.20
Total wolf	1,451	11.83	1.00	42.46	5.44	11.60-12.10
Hyena						
Andrés et al., 2012	1,145	3.28	0.35	31.60	2.55	3.14- 3.43
Delaney-Rivera et al., 2009	19	8.50	3.00	20.28	4.22	6.61-10.40
Total hyena	1,164	3.37	0.35	31.60	2.67	3.22- 3.52
Bobcat						
Delaney-Rivera et al., 2009	11	4.89	1.53	8.98	2.63	3.98- 5.80
Mountain lion						
Delaney-Rivera et al., 2009	33	10.46	1.60	31.31	7.22	7.99-12.92
Lion						
Andrés et al., 2012	200	9.84	2.70	35.00	5.06	9.13-10.50
Delaney-Rivera et al., 2009	12	8.60	1.97	19.27	5.73	5.36-11.84
Total lion	212	9.77	1.97	35.00	5.10	9.08-10.50
Bear						
Domínguez-Rodrigo and Piqueras, 2003	18	10.86	-	-	5.04	-
Schöningen, this study	179	11.77	2.95	34.13	5.51	11.00-12.60

Tab. 8 Reference data for carnivore tooth score lengths (mm): sample size (N), mean, minimum (Min), maximum (Max), standard deviation (SD), 95 % confidence intervals (95 % CI).

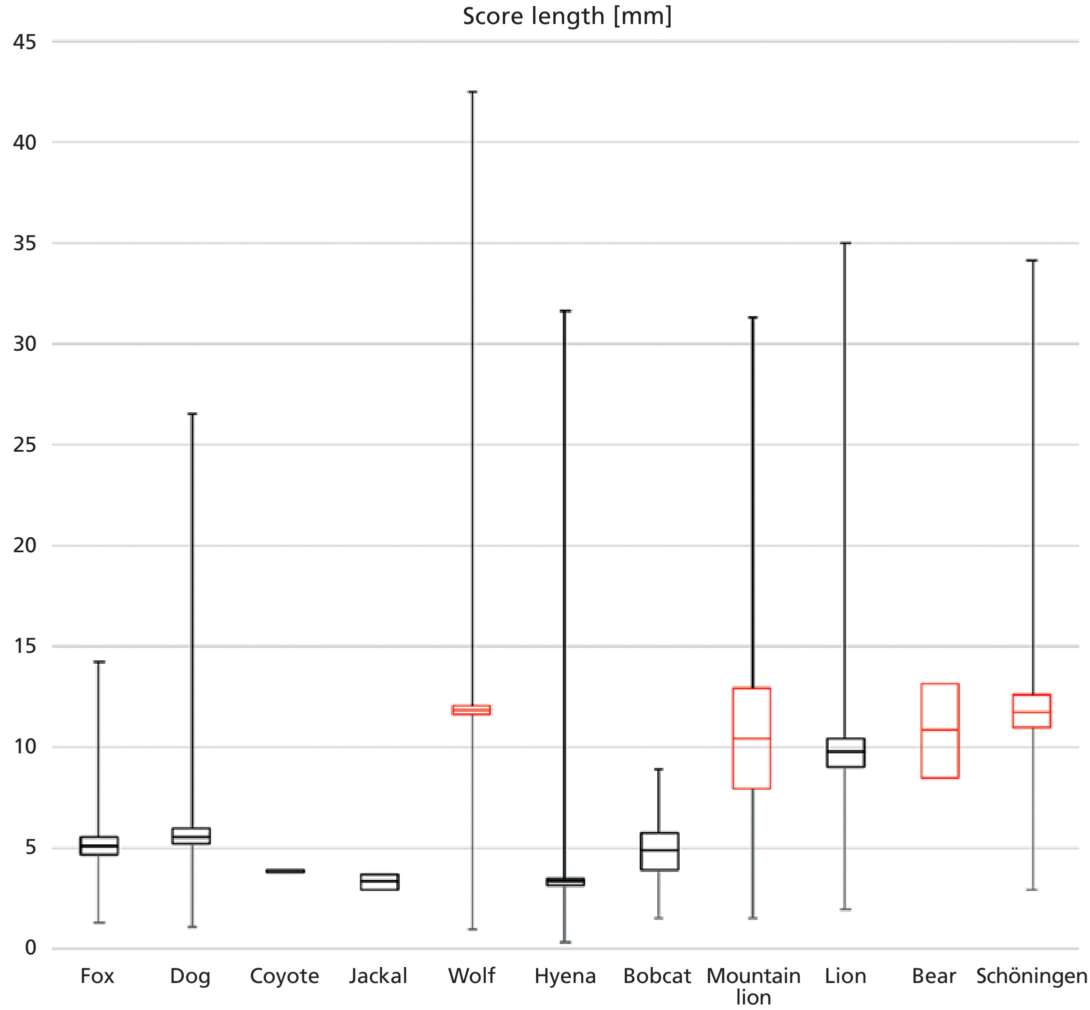


Fig. 21 Comparison of tooth score lengths among several carnivore species and the Schöningen sample. Data represent median score length with 95 % confidence intervals and minimum and maximum values from **Tab. 8**. Samples highlighted in red are not significantly different ($p \geq 0.05$) according to unpaired t-test.

CONCLUSIONS

From all available data, hominins are primarily responsible for the large accumulation of bones at Schöningen 13II-4 and the role of large carnivores in the formation of the site was as secondary scavengers. Cut-marks are far more prevalent than traces of carnivore activity and the locations of carnivore tooth pits and scores suggests secondary access to animal carcasses, at least for the large assemblage of horse bones. The nine bones with overlapping carnivore damage and butchery marks all show the carnivore tooth pits and scores on top of cut-marks, evidence for primary access by hominins and secondary scavenging by carnivores. Based on the faunal list and the large dimensions of tooth pits and scores observed on the gnawed ungulate bones, wolf and lion are suggested to be the primary scavengers of animal carcasses the Schöningen 13II-4. Between these two taxa, the heavy damage to many of the Schöningen bones and the consumption of some bone portions is more indicative of wolves than large felids.

A closer look at the finer details of the faunal assemblage reveals that carnivore marks are more prevalent on the appendicular skeletons of juvenile horses than adults. This pattern suggests that hominins fully

	Score breadth [mm]					
Reference	N	Mean	Min	Max	SD	95 % CI
Fox						
Andrés et al., 2012	103	0.44	0.11	2.02	0.33	0.37-0.50
Delaney-Rivera et al., 2009	2	0.50	0.46	0.53	0.05	0.43-0.57
Young et al., 2014	90	1.00	0.35	4.56	0.59	0.88-1.12
Total fox	195	0.70	0.11	4.56	0.55	0.62-0.77
Dog						
Andrés et al., 2012	209	0.69	0.14	4.58	0.32	0.65-0.74
Delaney-Rivera et al., 2009	18	0.72	0.20	1.46	0.34	0.57-0.88
Young et al., 2014	25	1.80	0.12	4.28	0.89	1.45-2.14
Total dog	252	0.80	0.12	4.58	0.53	0.74-0.87
Coyote						
Delaney-Rivera et al., 2009	1	1.09	-	-	-	-
Jackal						
Domínguez-Rodrigo and Piqueras, 2003	40	0.41	-	-	0.15	-
Wolf						
Sala et al., 2014	247	1.38	0.40	7.41	0.96	1.26-1.50
Campmas and Beauval, 2008	812	1.40	0.10	6.61	0.79	1.35-1.45
Andrés et al., 2012	384	1.93	0.12	7.91	1.34	1.80-2.07
Wolfspark Kasteelberg, this study	1,067	2.12	0.25	7.26	0.84	2.07-2.17
Total wolf	2,510	1.79	0.11	7.91	0.99	1.75-1.83
Hyena						
Andrés et al., 2012	1,145	0.63	0.10	9.00	0.68	0.59-0.67
Delaney-Rivera et al., 2009	19	1.37	0.81	2.28	0.47	1.16-1.58
Sala, 2012	105	2.84	0.50	25.00	3.41	1.84-3.83
Total hyena	1,269	0.82	0.10	25.00	1.32	0.75-0.90
Bobcat						
Delaney-Rivera et al., 2009	11	0.70	0.37	1.03	0.23	0.49-0.92
Mountain lion						
Delaney-Rivera et al., 2009	33	1.65	0.35	5.69	1.11	1.27-2.02
Lion						
Andrés et al., 2012	200	1.62	0.26	18.80	1.86	1.36-1.88
Delaney-Rivera et al., 2009	12	1.31	0.54	2.05	0.53	1.01-1.61
Sala, 2012	45	1.56	0.40	8.28	1.48	1.13-2.00
Total lion	257	1.60	0.26	18.80	1.75	1.38-1.81
Bear						
Domínguez-Rodrigo and Piqueras, 2003	18	1.77	-	-	1.29	-
Sala, 2012	21	1.88	0.40	4.70	0.95	1.48-2.29
Total bear	39	1.83	0.40	4.70	1.10	1.48-2.18
Schöningen, this study	179	2.14	0.62	7.61	1.13	1.98-2.31

Tab. 9 Reference data for carnivore tooth score breadths (mm): sample size (N), mean, minimum (Min), maximum (Max), standard deviation (SD), 95 % confidence intervals (95 % CI).

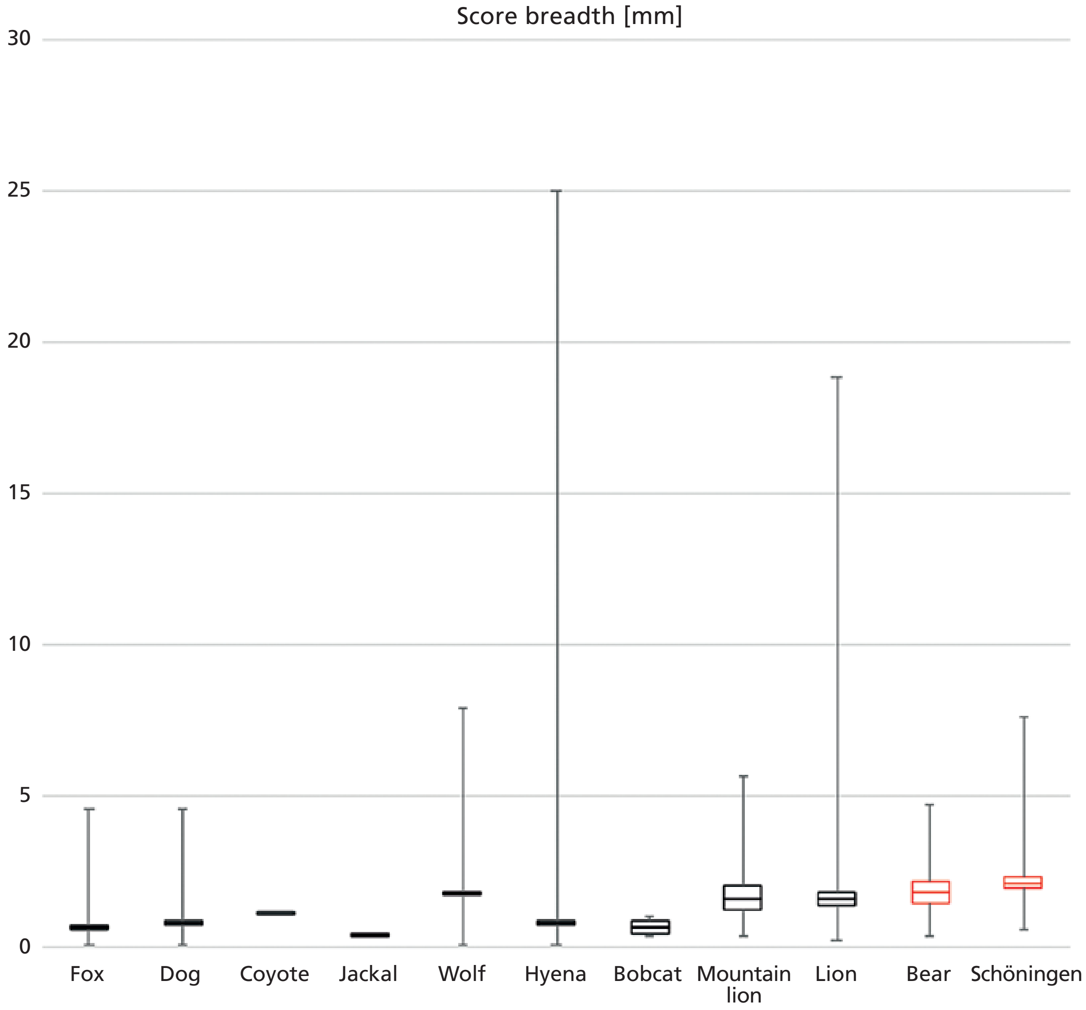


Fig. 22 Comparison of tooth score breadths among several carnivore species and the Schöningen sample. Data represent median score length with 95 % confidence intervals and minimum and maximum values from **Tab. 9**. Samples highlighted in red are not significantly different ($p \geq 0.05$) according to unpaired t-test.

processed adult horse limb bones for meat and marrow, but limbs of juveniles were discarded at an earlier stage of butchery, which may account for the greater incidence of carnivore damage to the appendicular skeleton of juvenile horses. Horse hunting at Schöningen appears to have targeted entire horse family groups; essentially, multiple horse individuals were killed at a time (Julien et al., 2015b; Hutson et al., 2020; García-Moreno et al., 2021). This echoes aspects of the "shoot first" and "adults only" hunting and butchery strategy noted at a number of Middle Pleistocene Neanderthal sites (Gaudzinski and Roebroeks, 2000; White et al., 2016), where prey mortality profiles include many prime-aged adults whose carcasses are extensively butchered, but the Neanderthals chose not to butcher the killed juveniles as thoroughly as the adults. In contrast to the horse assemblage, the much smaller red deer assemblage shows more carnivore damage than traces of hominin butchery. While red deer fall within the preferred prey size range of wolves in places where the two species co-occur (Newsome et al., 2016), we maintain that the red deer represented at Schöningen 13II-4 were hunted by hominins and subsequently scavenged by carnivores. Red deer form small social groups for most of the year and were likely killed individually rather than in entire family groups as reckoned for the horses. In consequence, there was less to scavenge from a solitary red deer carcass than there was from a butchery event involving multiple horses. Increased competition for the leftovers from single butchered red deer likely led to more completely scavenged carcasses, and therefore more carnivore damage to the remaining bones, increased consumption of some bone portions, and possible removal of some skeletal elements from the kill site. As for the very small bison and aurochs assemblage, hominins were only rarely successful in killing one of these very large and potentially dangerous animals. Modern lion prey preferences do include animals of this size (Hayward and Kerley, 2005) and bison fall at the upper limit of potential prey size for wolves (Newsome et al., 2016), but carnivore involvement with these species is limited to tooth marks on only a few remains and is therefore reasoned to represent scavenging from hominin kills.

The site's vast area and high density of faunal remains within the main concentration pose complications for interpreting spatial aspects of hominin and carnivore activities (see Böhner et al., 2015; Peters and van Kolfschoten, 2020; García-Moreno, 2021). However, here we have noted that spatial relationships may be more apparent in the eastern portion of the site where the density of faunal remains is lower. Away from the main concentration, clusters with more carnivore-marked bones are slightly offset from those clusters with more cut-marks, scraping marks, and impact damage. Similarly, the Carnviore/Butchery Index reveals scatterings of carnivore-damaged bones around the periphery of denser clusters of hominin-damaged bones. This can be taken as further evidence of carnviores scaveneging and scattering of some bones from hominin kills. Dispersal of bones from large mammal carcasses by wolves is usually limited to less than 15 m (Haynes, 1982), although wolves may transport some bones greater distances, especially if single carcasses are scavenged multiple times (Yravedra et al., 2012). With future work, it may be possible to piece together individual kills from among these less-dense clusters of hominin- and carnviore-damaged bones. In turn, this would serve as a model for disentangling discreet hunting events within the main concentration at Schöningen 13II-4 and further afield at other sites across the broader Schöningen lakeshore environment.

We have argued here that hominins were the dominant predator on the Schöningen landscape. The impact of carnivores on the Schöningen 13II-4 faunal assemblage was secondary to that of hominins, and wolves were the primary scavengers of hominin kills. Based on the relatively undisturbed nature of the Schöningen 13II-4 deposit, wolf access to prey carcasses followed in quick succession after abandonment by hominins. Such events were probably commonplace during the Middle Pleistocene in Europe, but what is intriguing about the scenario at Schöningen is that wolves consistently scavenged from hominin kills at the same open-air lakeshore location. Hominins and wolves did not exist in isolation from one another, but rather they shared the Schöningen landscape. Wolves are not obligate scavengers, but high-ranking predators, and any encounters with hominins were likely to have been aggressive. Yet, these adversarial relationships between predators were built on mutual respect and caution born from generations of co-habitation, possibly involving some level of wolf habituation to hominins. Habituation is a key element of the commensal pathway toward domestication (Zeder, 2012), wherein wild species may become increasingly reliant upon human-mitigated landscapes for survival. We are not suggesting that Middle Pleistocene hominins at Schöningen domesticated wolves, but the primordial elements of this special relationship existed on the Schöningen landscape. Thousands of years of sustained habituation eventually drew humans and wolves ever closer into a mutually beneficial partnership that culminated in the appearance of domestic dogs by the Last Glacial Maximum.

Acknowledgements

Elaine Turner is fond of wolves, and other carnivores, too, but mostly she is fond of wolves. This trait was on full display during our visits to *Adler- und Wolfspark* Kasteelburg that she most eagerly coordinated. Under different circumstances, Elaine would be included as a co-author on this *Schrift*; instead, we offer this *Festschrift* in honour of Elaine and the work she holds so dear. Elaine has been deeply involved in the Schöningen project at MONREPOS from the beginning. She was the main driving force behind the practical organisation of research and continues to be a major asset in communication among everyone involved with Schöningen research at MONREPOS. In other words, Elaine is the glue that has kept this Schöningen project going for nearly a decade, always sharing knowledge, always practical, always reliable, and always gracious.

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