

## Research Article

# Extinctions of Late Ice Age Cave Bears as a Result of Climate/Habitat Change and Large Carnivore Lion/Hyena/Wolf Predation Stress in Europe

**Cajus G. Diedrich**

*Paleologic, Private Research Institute, Petra Bezruce 96, CZ-26751 Zdice, Czech Republic*

Correspondence should be addressed to Cajus G. Diedrich; [cdiedri@gmx.net](mailto:cdiedri@gmx.net)

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Predation onto cave bears (especially cubs) took place mainly by lion *Panthera leo spelaea* (Goldfuss), as nocturnal hunters deep in the dark caves in hibernation areas. Several cave bear vertebral columns in Sophie's Cave have large carnivore bite damages. Different cave bear bones are chewed or punctured. Those lets reconstruct carcass decomposition and feeding technique caused only/mainly by Ice Age spotted hyenas *Crocota crocota spelaea*, which are the only of all three predators that crushed finally the long bones. Both large top predators left large tooth puncture marks on the inner side of cave bear vertebral columns, presumably a result of feeding first on their intestines/inner organs. Cave bear hibernation areas, also demonstrated in the Sophie's Cave, were far from the cave entrances, carefully chosen for protection against the large predators. The predation stress must have increased on the last and larger cave bear populations of *U. ingressus* (extinct around 25.500 BP) in the mountains as result of disappearing other seasonally in valleys migrating mammoth steppe fauna due to climate change and maximum glacier extensions around 22.000 BP.

## 1. Introduction

**1.1. Cave Bear Research History in Germany.** Many incomplete cave bear bones from the Late Pleistocene Ice Age (113.000–22.000 BP) have been found in Europe and focussed herein in Germany mainly from 42 famous cave sites but also a smaller number from open air sites (Figure 1(a)). The cave bear bones show always similar patterns of damage [1–3] including bones from the new described Sophie's Cave site in Upper Franconia, Bavaria (Figure 1(b)) and the not far situated famous Zoolithen Cave with its Late Pleistocene herbivorous [4] cave bear "*Ursus spelaeus* Rosenmüller 1794" [5], whose holotype skull was recently rediscovered [6]. This most famous bone-rich Zoolithen Cave of central Europe with its long history of "cave bear bone hunt" [7] has also yielded the holotype skulls of predators such as the Ice Age spotted hyena *Crocota crocota spelaea* (Goldfuss 1823) [2, 8, 9], the steppe lion *Panthera leo spelaea* (Goldfuss 1810) [8, 10, 11], the "cave wolverine" *Gulo gulo spelaeus* (Goldfuss 1818) [12], and the "cave wolf" *Canis lupus spelaeus* Goldfuss 1823 [9].

**1.2. The Upper Franconian Caves and the Studied Sophie's Cave.** Close to the Zoolithen Cave one new Late Pleistocene megafauna key locality is presented herein within the discussion about "cave bear den bone taphonomy" in Europe, the Sophie's Cave (Figure 1). This show cave has a long history and was also named historically "Rabenstein Cave," "Clausstein Cave," or "Ahorn Cave" [13]. The anterior cave areas were already visited by the priest Esper [14] who tried to establish the "great deluge," on German Upper Franconian Caves near Muggendorf [11, 15], bone accumulations in caves, mainly at the Zoolithen Cave. Also Rosenmüller [16], and later Goldfuss [11], collected bones in the Sophie's Cave, but much more in the Zoolithen Cave, when they did mainly research on the Zoolithen Cave cave bears. Buckland [13] was Esper's main "antagonist," and used the large portal cave directly opposite the Sophie's Cave, the former called "Kühloch Cave" (today = König-Ludwigs Cave, Figure 1(b)) to establish bone accumulations in caves to be mainly of "hyena origin." He was the pioneer of "Ice Age cave hyena den research" and described even phosphatic pellet layers and chewed bones from the König-Ludwigs Cave, whose sediment and material

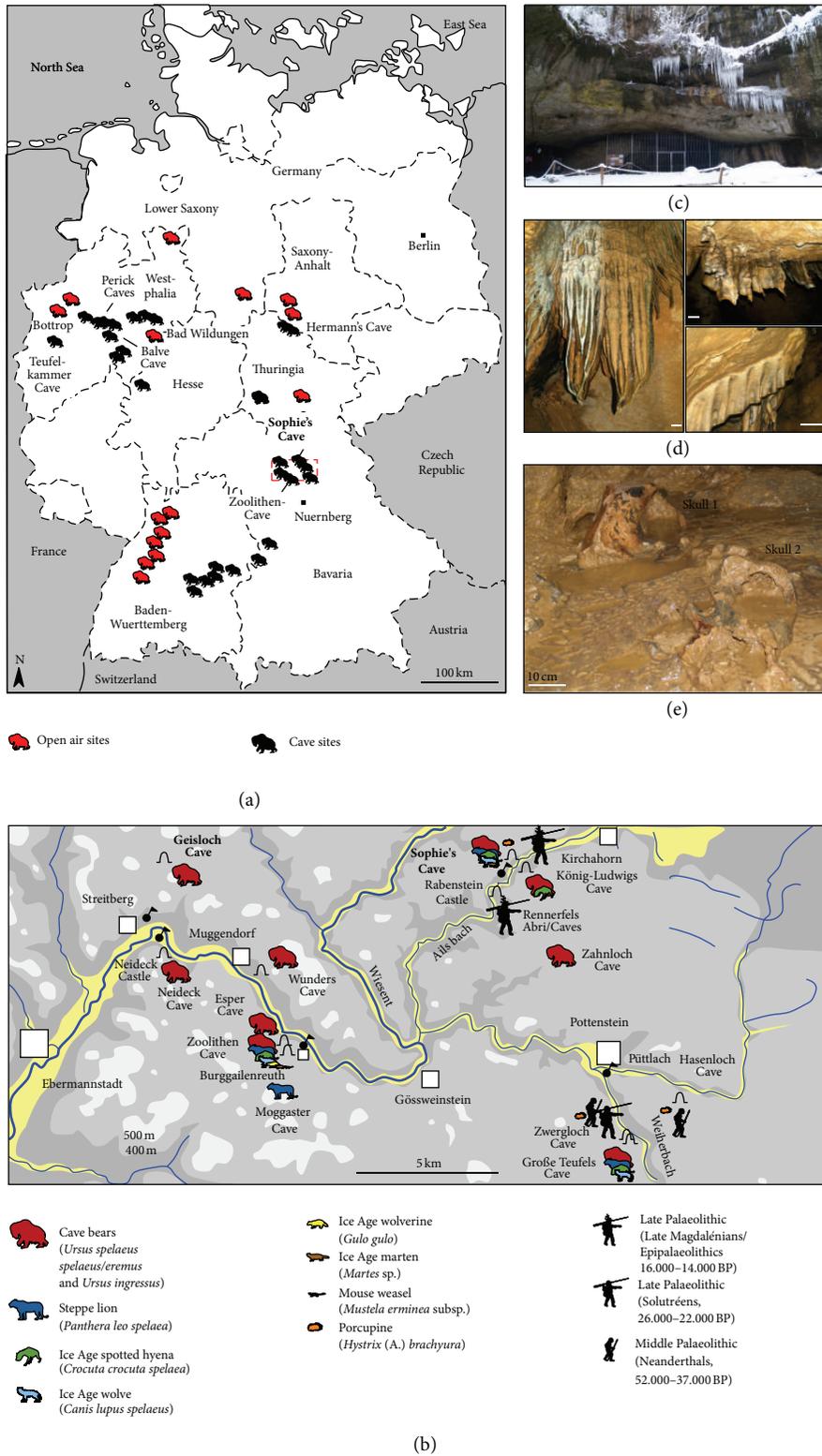


FIGURE 1: (a) Geographical locations of German cave bear sites, both cave den and open air sites, including Sophie’s Cave in Bavaria, southern Germany. (b) Cave map showing cave bear, hyena, and wolf den areas during the early/middle Late Pleistocene in Upper Franconia (Bavaria, Germany). (c) The present-day entrance of Sophie’s Cave. (d) Speleothems in the Millionary Hall of Sophie’s Cave. (e) Two cave bear skulls (small types: *Ursus spelaeus* subsp.) fixed in the speleothem layer of the Reindeer Hall of the Sophie’s Cave (on place).

was sadly removed in historic times, after Buckland's first visits. The history and several cited passages concerning discovery and finds of the Sophie's Cave are recently reviewed [17].

Whereas in historical times after 1833, when the part behind the Sand Chamber of the Sophie's Cave was opened [22, 23], parts of the cave interior were destroyed, only few and about 40 cave bear, one hyena and one lion skull were found in the Reindeer Hall (old name = "Erste Abteilung"), of which most were taken somehow after 1833, which became a part of collection in the nearby Rabenstein Castle that finally got lost in 1978 mostly (all skulls) when the owner changed [17].

A cave survey or systematic excavations never have been made before 2011. Whether cave sediments nor fossil contents were dated in former times, neither bones were understood in the taphonomy. No Pleistocene animal species were determined exactly such as coprolites were unknown. Only historical literature was compiled of former historic articles. The only "unusual" find besides the dominant cave bear remains was the discovery in the Sophie's Cave of many reindeer antlers after Münster's unpublished report in 1833 (mostly shed ones, already repeated [24]) and a mammoth pelvic was found only in the Reindeer Hall. One of the pelvic halves (=coxa) seems to have been removed historically; a second half (another coxa) was excavated and prepared within the new campaign. This reindeer antler taphonomy is still in human origin discussion, but hyenas and wolves as accumulators of more than 100 shed and selected large male antlers must be excluded, whereas a "shamanic background of Late Magdalénians/Epipalaeolithics" in the final Ice Age has to be considered most [25].

Whereas in another publication [25] the sedimentology, valley, and cave genesis were studied in detail, the Pleistocene fauna is presented with taphonomically comparison to other Upper Franconian and mainly German cave bear den caves. Another target is the cave bear material dating, which indirectly dates the sediment layers in the cave. Finally the question of the cave use in different areas and during different periods by several mammals such as mustelids, cave bears, hyenas and sporadic dwellers like wolves and lions, and all their ecological behaviours and interactions is analysed, compiled, and reviewed from former studies and compared to many caves of central Europe, especially the Zoolithen Cave. The taphonomic study of the bones themselves follows not the classical bite damage or bite mark analyses [27–29], instead the repeating bone damage types and different stages on modern African mammals [30], Pleistocene cave bear bones [1, 3, 31], woolly rhinoceros bones [3, 32–34], or elephant bones [35] were used. Those latter analyses include the carcass decomposition strategy of hyenas, which is highly important to distinguish between hyena and non-hyena damage origin. For sure, both are important to use and to identify the carnivore group or even the exact predator or scavenger. A final predator guild structure (sensu [36, 37]) cannot be yet completed, because herein the wolverines and leopards are not studied or included in the cave bear predatory study. Herein it will be demonstrated that there is a relationship

between predators and two main different megafaunas in different palaeoenvironments of central Europe.

## 2. Material and Methods

Between January and July 2011 a new, interdisciplinary cave survey of the Sophie's Cave allowed the cave's history since the Pliocene to be reconstructed, including its refilling during the Pleistocene as a result of its location along a river valley. The cave was explored geologically, palaeontologically, and archaeologically in order to understand its use by animals during the Pleistocene. Middle Pleistocene mustelid tracks and Late Pleistocene megafauna remains, mainly cave bear bones (more than 1,600), were found during this exploration. In some parts of the cave these remains were excavated systematically and placed into a stratigraphic context. Dating was possible by the sedimentological stratigraphy and by analysing the evolution of cave bear tooth morphology. Some of the excavated bones presented herein are from the Reindeer Hall, but most are from the Bear's Passage, which also provided the most important material for this study in the form of wolf remains, wolf coprolites, and many chewed and damaged cave bear bones, all of early to middle Late Pleistocene age (Figures 3 and 4). Wolf and hyena scat was compared to that of modern and Pleistocene subspecies. The large quantity of wolf material from Zoolithen Cave and a little material from other caves in surrounding areas were also studied in order to understand the palaeoecology and bone taphonomy. Some thousands of bones were included in the comparative study of five important open air and cave sites to obtain a cross-section of bone accumulations from different elevations and palaeoenvironments. In particular, the repetitive patterns of damage by carnivores on cave bear bones from more than 42 German caves and some open air sites (Figure 1) were compared. The material from Sophie's Cave is housed in the museum of the Castle Rabenstein (<http://www.burg-rabenstein.de/>), and in several cases it was left in situ in the show cave (Bear's Passage, Reindeer, and Millionaire Halls).

## 3. Results and Discussion

*3.1. Cave Genesis, Sediments, and Dating.* It was already remarked [38] that cave sediments of caves along valleys are important for the landscape reconstruction and Upper Franconia dewatering system of the Pleistocene. First identifications of river terraces of the Franconian Karst were made in the Franconian Pegnitz valley [39], but with a coarse model. A first new discussion about river terraces in Upper Franconia appeared with the new sedimentological research of the Zoolithen Cave along the Wiesent Valley, where 140 meters above today's river elevation the entrance must have been flooded after 35,000 BP, dated by cave bear tooth morphology and stratigraphy [2]. Obviously the Zoolithen Cave had been flooded (as already thought by Esper [14], but there is a different "biblical scenario"), and river terrace coarse dolomite pebbles were deposited in the main hall, in which the replaced most of the bone layers, which latter accumulated in bonebeds in strong flood events into the

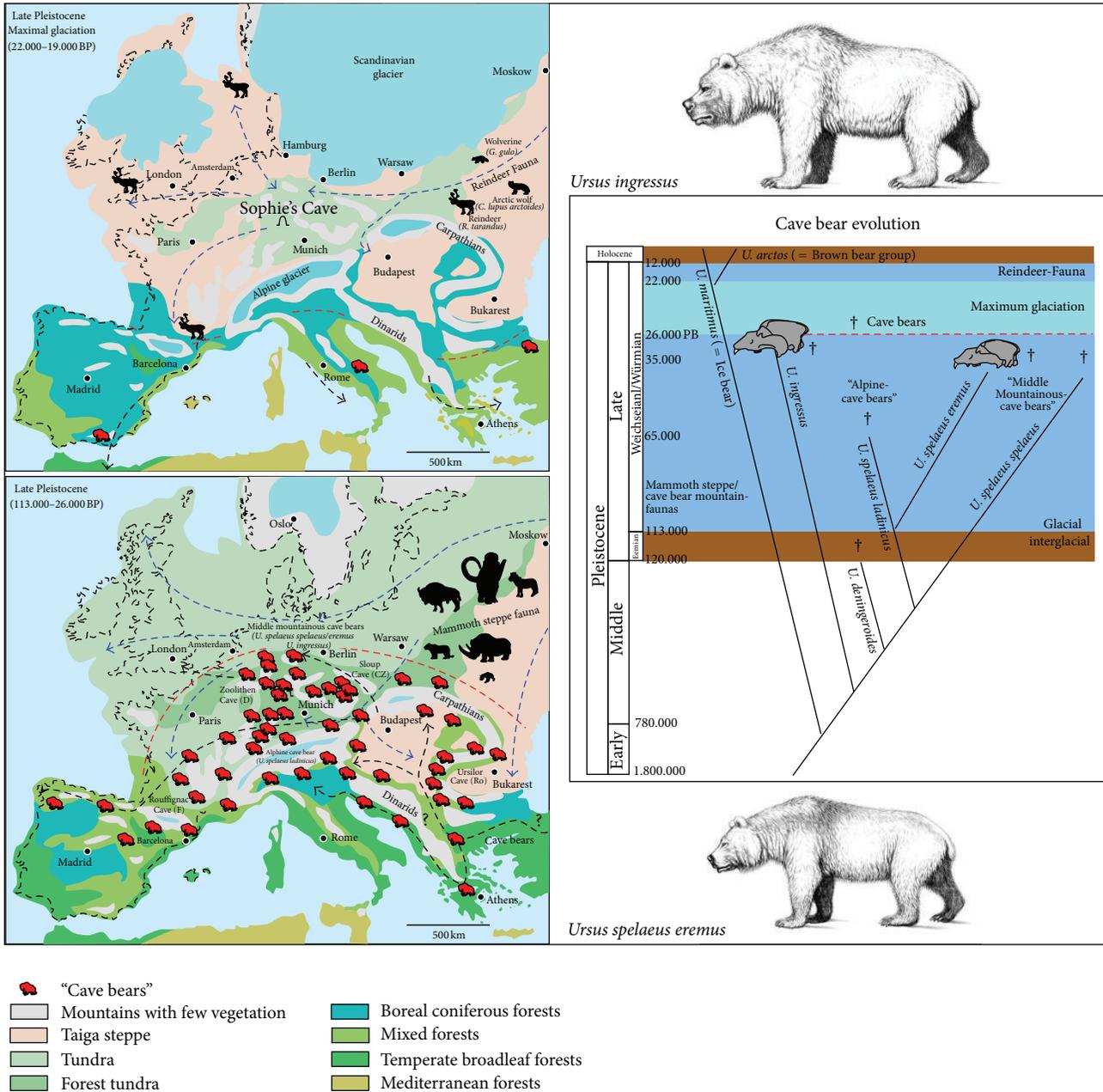


FIGURE 2: (a) Cave bear biogeography and possible migration models, evolution, and extinction with faunal exchange in Europe with the main different models ("cave bear" illustrations by G. "Rinaldino" Teichmann; Graphics: PaleoLogic) (cave bear evolution composed after [18–21]).

vertical shafts all over the middle part of the cave system, even up to 30 meters deep [2]. The question remains; how did the Wiesent Valley form after 35.000 BP, eroding 140 meters deep, whereas postglacially (after LGM, 24.000 BP) the river terrace during the latest Late Pleistocene was already on today's elevation demonstrated by Late Magdalénian to Epipalaeolithic abri camp sites along the Wiesent and Ahorn Valleys [25]. Further caves have to be studied, but visits of caves in similar elevations around the Muggendorf Wiesent Valley have delivered similar terrace dolomite gravels in

other similar elevated caves. Therefore, a river terrace must have existed, and the valley must have been eroded quickly, however.

A first sedimentological study in the Sophie's Cave was made [25], of which herein only the main results are presented. Die Sophie's Cave eroded into massive Upper Jurassic sponge-reef-dolomites such as all caves in the surrounding of Franconian village Muggendorf [15, 40] whereas the branches within the cave system are oriented on larger NNO-SSW cleft systems.

Cave bear tooth and skull morphology and dating

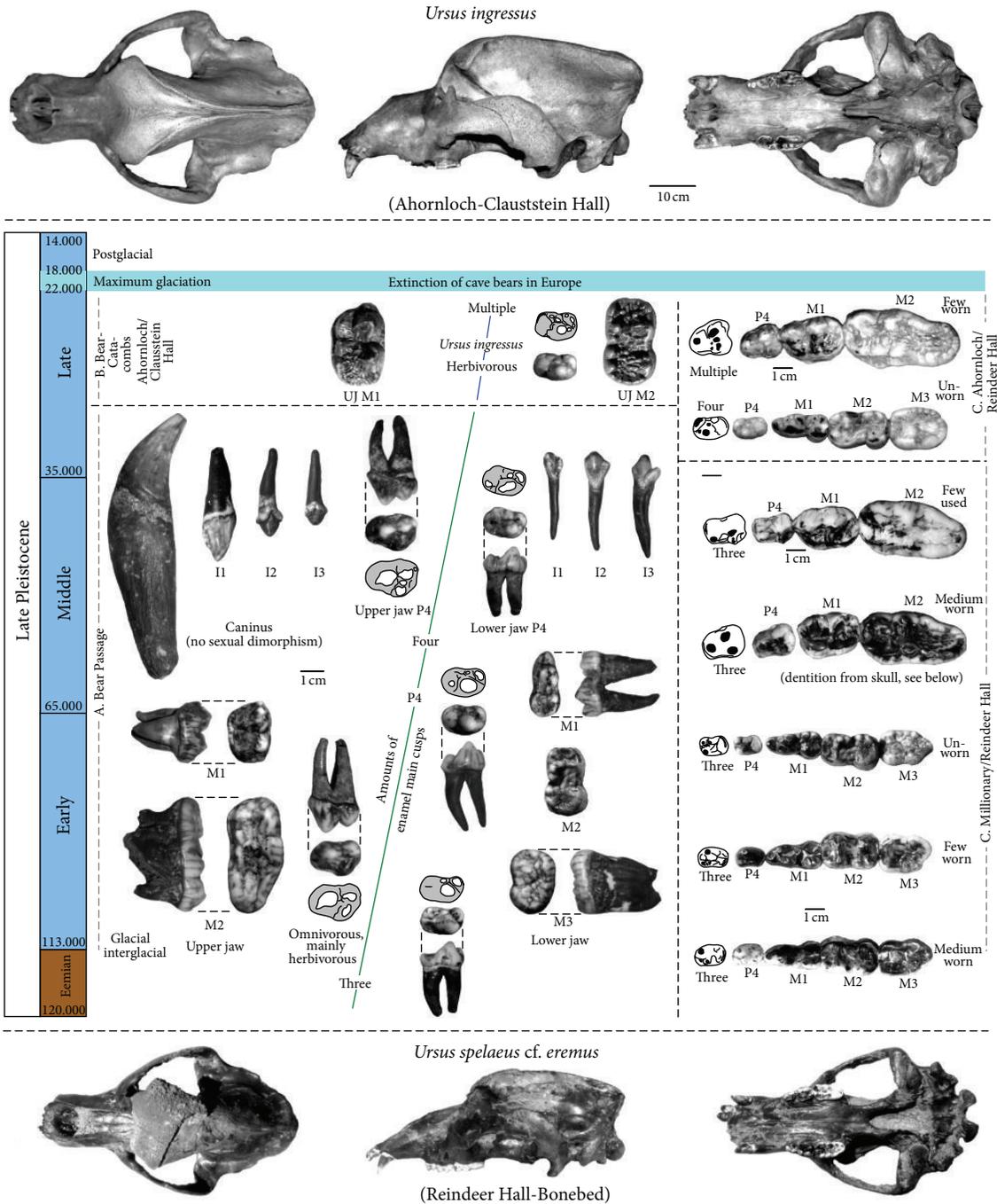
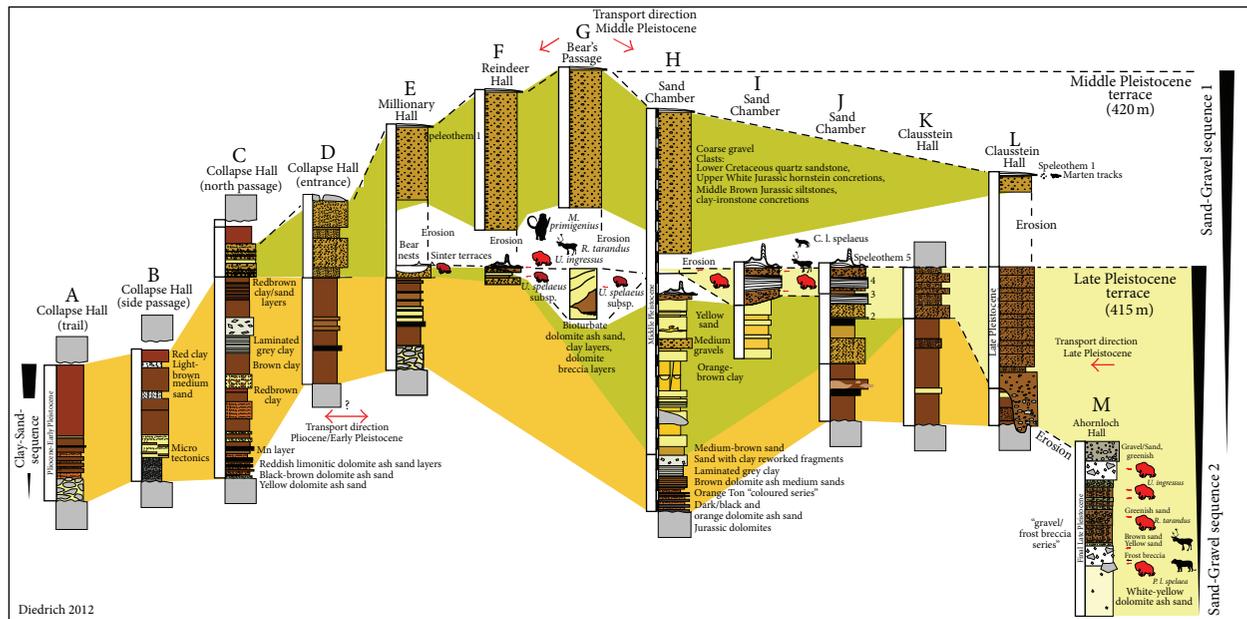


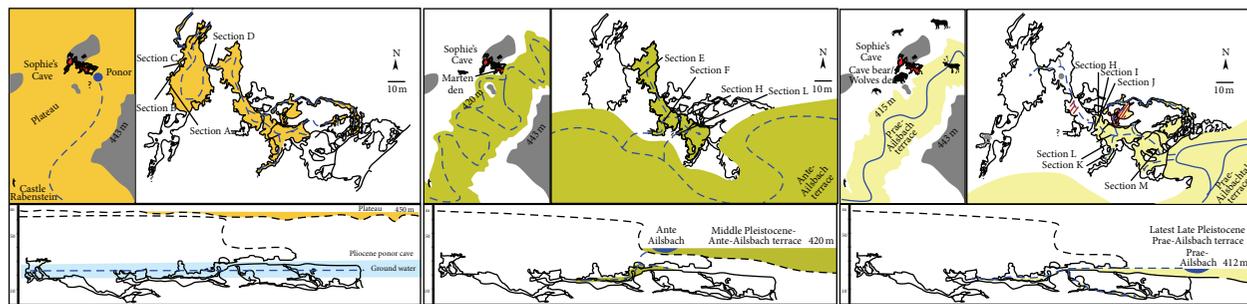
FIGURE 3: Cave bear species/subspecies and dating for the Sophie’s Cave cave bear material with the tooth morphology method [26] and skull morphology [19]. Teeth of *U. spelaeus* subsp. (*eremus/spelaeus*) from the Bear’s Passage, Millionary, and Reindeer Halls date into the early-middle Late Pleistocene. Teeth from the Bear’s Catacombs, Ahornloch/Claustein Halls are *U. ingressus* forms of the late Late Pleistocene. Skulls of the Reindeer Hall bonebed are only from the early Late Pleistocene, whereas large *U. ingressus* skulls from the Ahornloch/Claustein Halls again date to the late Late Pleistocene.

3.1.1. Pliocene-Early Pleistocene. Within the ground water phreatic system of the Pliocene Plateau (elevation 450 a.s.l., Figure 4(b)), an underground stream formed the cave, in three levels, whereas for fluvial waters typical facets [41, 42]

are preserved on the Sophie’s Cave ceilings, especially in the last halls, the Millionary, and Collapse Halls. Parts of the cave were simultaneously filled with the first sediments within the Pliocene to Early Pleistocene. The sediments



(a) Sophie's Cave sections



(b) Pliocene-Early Pleistocene

(c) Middle Pleistocene

(d) Final Late Pleistocene

FIGURE 4: Stratigraphy, cave infill history, and palaeoenvironment/valley genesis reconstructions. (a) Sections. (b) Pliocene-Early Pleistocene cave erosion and first sedimentary filling. (c) Middle Pleistocene river terrace sediment infill, and (d) latest Late Pleistocene river terrace sediment infill. (Early to Middle Late Pleistocene; see Figure 5).

are typical for caves [43, 44] and are fine-grained river deposits with coloured sequences consisting of red-brown clays, dark manganese layers, yellow dolomite ash (from dolomite weathering (see [45])), sand, and silt layers. Those coloured sediments and the cave were tectonically rotated about 1-2° in the Middle Pleistocene.

**3.1.2. Middle Pleistocene.** The first river terrace deposits of the Pre-Ailsbach River of the Ahorn Valley (elevation 420 a.s.l., Figure 4(c)) flooded only the areas over the Reindeer Hall (from above), whose sediments were also washed into the Clausstein, and Millionary Halls, only (Figure 4(c)). The up to 8 meters thick terrace sequence starts on the bottom with thick partly mud cracked yellow-brownish clay, and silt-sandstone dolomite ash layers which are flooding deposits (sensu [44]). Within the filling of the valley, the terrace moved few upwards and transported river gravels of 1-3 meters thickness into the cave. Middle and Upper Jurassic ammonite and fossil fragments, and Jurassic Flintstones (fossilized

sponge), and siltstones, but also Lower Cretaceous river quartzite (secondary reworked), which were eroded north, allowed the reconstruction of the river flow direction to the south. Most of those sediments reach up to the elevation about 415 a.s.l., which were finally covered by the first up to 20 cm thick speleothem layer (older generation see [25]), were eroded together within the Middle Pleistocene. At this time, the first cave entrance was opened (Bear's Passage entrance, today blocked), which was used later in the Late Pleistocene by cave bears and carnivores.

**3.1.3. Late Pleistocene.** The Bear's Passage was, however, dry and only dolomite ash sand and dolomite blocks were deposited. The cave bears are dated and attributed by their P4-tooth morphology with dominance of three-coned morphotypes (method see [26]) to the early middle Late Pleistocene small forms of *U. speleus eremus/spelaeus* (Figure 3). The second terrace formed (about 425-420 a.s.l.) during the latest Late Pleistocene. This fluvial Pre-Ailsbach river sequence

starts with sands and silts, but primary is built up of terraces quartz sands/silts which were transported into today's entrance cave area (Ahornloch Hall) only into the first chambers, halls, and branches of the Sophie's Cave (Figure 4(d)). The upper layers consist of gravels, even containing larger blocks in the Ahornloch Hall (Figure 4(a)). While the lower sand series date to the late Late Pleistocene with cave bear teeth of the large cave bears *U. ingressus* (Figures 3 and 4(a)), the uppermost gravels were washed up into the Sand Chamber only and are nearly without bone content. The flooding (see similar structures in [44]) washed most of the bones of the Ahornloch and Clausstein Halls into the lower parts of the Ahornloch Hall, Clausstein Hall, and the Bear's Catacombs. Those floods destroyed also parts of the middle parts of the sections and sediment sequences of the Middle Pleistocene and "intercalate" into those (Figure 4). A single lower jaw found attached below the latest speleothem layer about 16.000–12.000 BP, (see [25]) date precisely a younger and larger cave bear (*U. ingressus*), from those (*U. s. spelaeus/eremus*) which were found below the speleothem layer in sands and clays. Within the speleothem layer of the Reindeer Hall (and also Sand Chamber) many shed reindeer antlers were encrusted somehow after 16.000 BP [25]. Today, the valley is on an elevation of 375 a.s.l., and post maximal-glacial, the valley must have eroded about 40–50 meters deep.

**3.2. The New Sophie's Cave Bone Discoveries.** The first use of the Sophie's Cave as a den by cave bears appears to have been during the Eemian interglacial, continuing through the early to middle Late Pleistocene (about 120.000–35.000 BP) using the cave genesis, sedimentary infill and correlation of the sections (two river terrace sequences), and dating by cave bear teeth (Figures 3 and 4). Eight cave bear hibernation beds are still preserved in the deepest accessible parts of the cave, known as the Millionary Hall (Figures 5(d) and 5(e)). More than 50 cave bear skulls and thousands of bones accumulated in a bonebed layer that occurs in the Millionary Hall, the Reindeer Hall (Figures 5(b) and 6), and the Bear's Passage (Figure 10(a)), when the cave was still accessible through its original entrance, which has subsequently been blocked (Figures 4 and 5). The bones in this bonebed are from only three species: the small cave bear subspecies *Ursus spelaeus* cf. *eremus*, the Ice Age wolf *Canis lupus* cf. *spelaeus*, and the mustelid *Mustela erminea* (Figures 10(a) and 10(b)). The presence of hyenas and lions as cave dwellers is, however, also indicated by the indirect evidence of bite marks and abundant bone damage (Figures 6, 7, 8, and 9). A hyena skull and the lower jaw of a lion have been reported historically from the Reindeer Hall but can no longer be located. During the youngest early to middle Late Pleistocene (about 35.000–24.000 BP), the Sophie's Cave cave bear den was only accessible through the present entrance in the Ahornloch Hall, because the former entrance through the Bear's Passage had become blocked (Figure 4). In the final years of its occupation the Sophie's Cave cave bears (during the late Late Pleistocene) were used by a different, giant, European cave bear (*Ursus ingressus*) which replaced the smaller forms (Figures 2–4), but these also show similar patterns of bone damage and abundant bite marks not only

on cub remains. Finally, all three of the last (Late Pleistocene) European predators *P. leo spelaea*, *C. crocuta spelaea*, and *C. lupus* cf. *spelaeus* are represented by sparse bone records from the Ahornloch Hall that formed the entrance area during the latest Late Pleistocene. During the same period, hyenas are also known to have used the König-Ludwigs Cave, which is located opposite to the Sophie's Cave (Figure 1(b)), as a den, and the Zoolithen Cave a few kilometres away is known to have been used as a cub-raising den by hyenas [2] as well as the Große Teufels Cave (Figure 1(b)). Clans of these last hyenas of Europe were present in this region at this time with populations over longer periods.

With the new Pleistocene megafauna discoveries in the large cave bear den at the Sophie's Cave (Figures 1(b)–1(e)), wolves can for the first time be added to the hyenas and lions [1, 3, 10, 46, 47] as large Ice Age predators and scavengers feeding on cave bears.

**3.3. Bite Marks and Damage Patterns on Cave Bear Bones.** The characteristics of many bite marks [48] as well as their size (in particular of those on the vertebral columns of the Sophie's Cave cave bears, and large canine impact marks; Figures 6–9 and 13) exclude the possibility of these having been caused by wolves (Figure 13), but this is not always the case. Small and large carnivore bite marks appear in the prey bones of all three predators, as shown herein, with jaws, dentitions, and bite marks differing according to their specialized functions for meat eating, cartilage chewing, or bone crushing (Figure 13). The suggestion that cave bears produced cannibalistic major bone damage and holes in bones [49–51] can be dismissed because their grinding dentition was adapted for a fully herbivorous diet [4]. Even the suggestion that large holes in the compacta shafts of juvenile cave bears were evidence of "bone flutes made by Neanderthals" is already revised as these holes were simply punctured by the premolars of hyenas, without them being cracked because of the low level of calcification in juvenile bones [1, 3].

An analysis of the types of herbivore bone damage caused by modern African [30] and Ice Age spotted hyenas, looking for repeating patterns of damage, included large quantities of bones from hyena den sites or overlapping hyena and cave bear den sites [1, 3, 52]. The bone damage found regularly in the cave dens of cave bears across Europe was at first attributed mainly to hyenas [1, 3, 52], but later the hunting activities of lions were also recognized as having also played a part, albeit to a lesser extent [10]. Large quantities of cracked long bones and characteristic puncture marks can only be attributed to hyena activity, and in particular the use of their cracking teeth, the premolars (Figure 13).

The third large predator, the Ice Age wolf (*Canis lupus* cf. *spelaeus*), is known from over much of Europe including the studied region (Figures 1(b) and 10) and also used particular parts of caves for cub raising during the Pleistocene [53]. These wolves have been less well studied and it was not previously clear if they also consumed or killed cave bears in their caves.

**3.4. Wolf Bones and Den Marking Faeces.** Some of the coprolites from the Sophie's Cave (Figure 11) were found in situ,

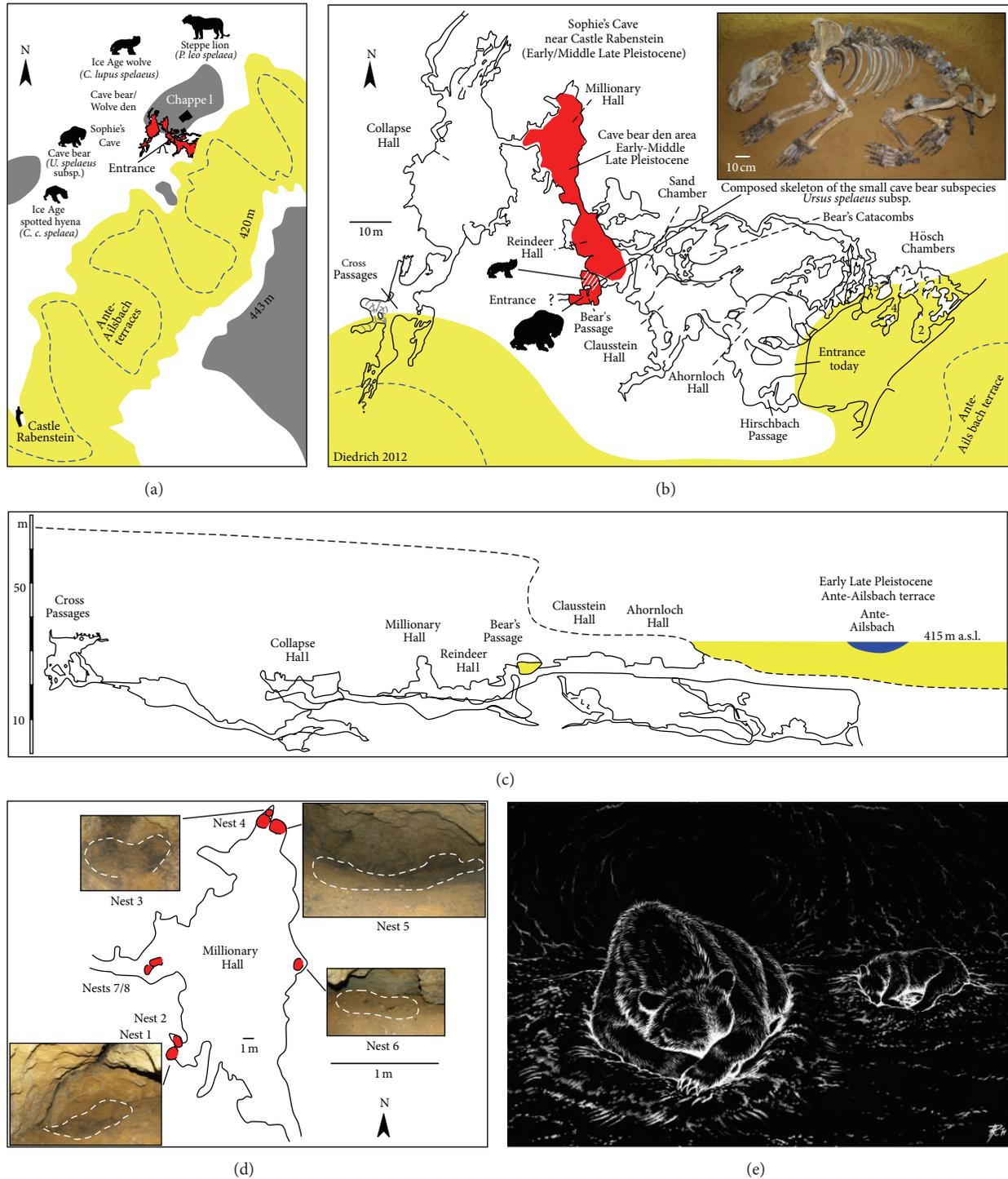
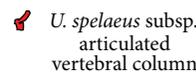
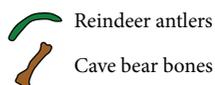
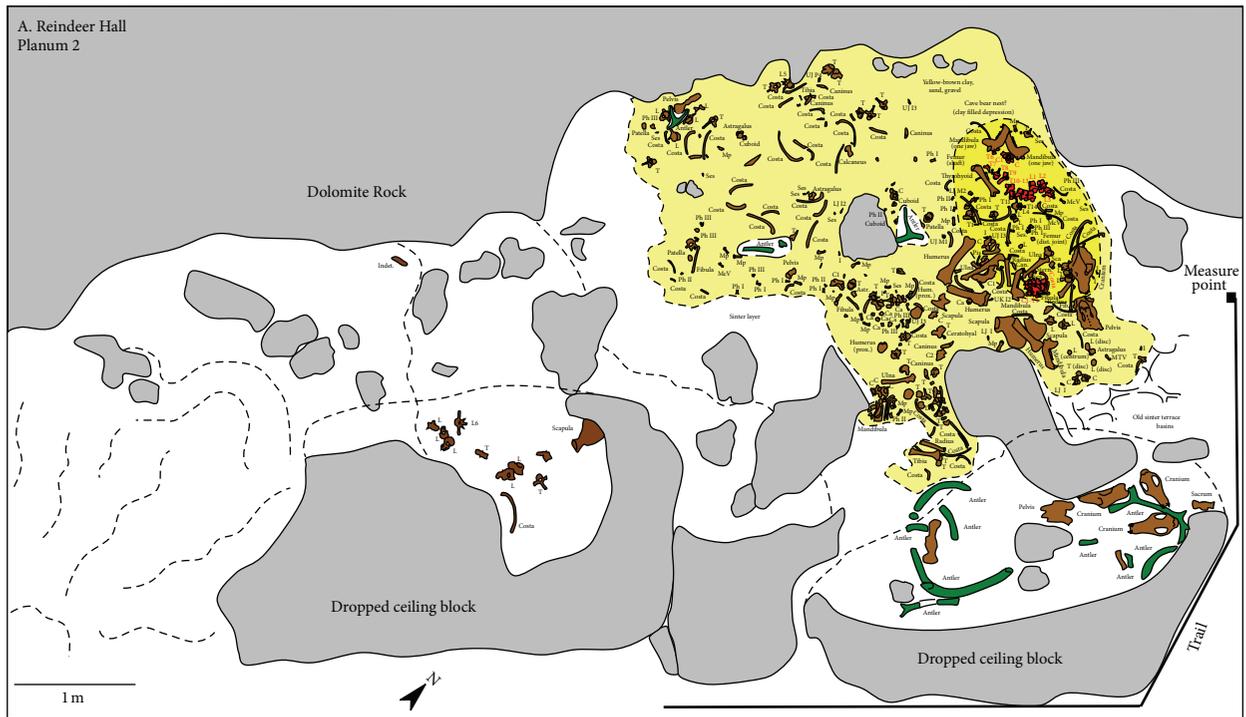


FIGURE 5: (a) Reconstruction of the geomorphology and Ante-Ailsbach River terrace of the Ahorn Valley. (b-c) Cave map: abundant cave bear bones were found in the areas marked in red, of which a skeleton was reconstructed from bones found in the "Bear's Passage," which was also partly used as a wolf den and contained many coprolites and wolf remains. (d) Eight preserved cave bear nests deep within the Sophie's Cave (Millionary Hall). (e) Hibernating cave bear mother and cub (Illustration: G. "Rinaldino" Teichmann).

together with wolf, cave bear, and mustelid bones (Figures 10(a) and 10(b)).

Of the wolf bones recovered, 52 were from the distal part of the Bear's Passage (Figures 10(c), (2)–(35)) and

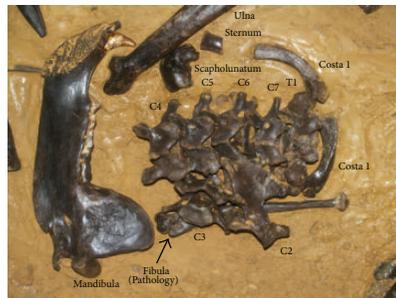
have recently been recognized as belonging to a single individual: an adult *Canis lupus* cf. *spelaeus* (Goldfuss 1823) with pathological damage (middle thoracic vertebra, dorsal spine damage, Figure 10(c), (4)). This is a large Ice Age wolf



(a)



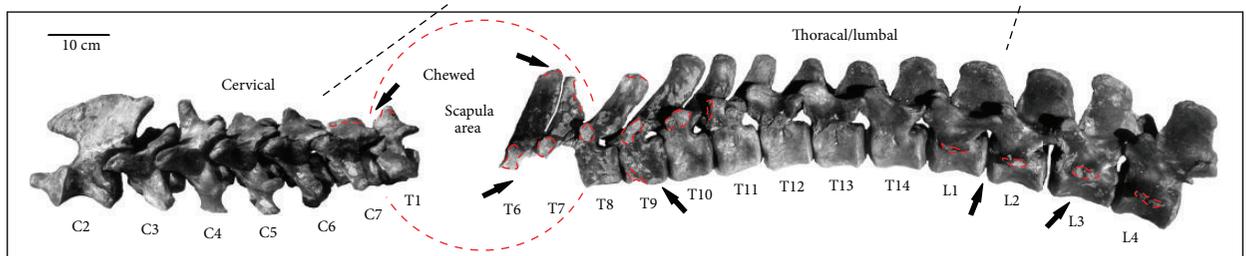
(b)



(c)



(d)



(e)

FIGURE 6: (a) Cave bear bonebed after excavation in 2011 in the hibernation area “Reindeer Hall” (Reindeer Hall) of the Sophie’s Cave and (b–e) articulated cave bear vertebral columns with bite damages (possibly one individual).

subspecies similar to the Canadian arctic-boreal mountain-adapted timber wolf [54] that has not yet been well defined by DNA [55]. Wolf populations are also known from other caves in the area (the Zoolithen and Große Teufels Caves,

Figure 1(b)). Their dens have also been identified, especially in the Zoolithen Cave which had a large population and has yielded more than 380 bones (Figure 14(a)) as well as several skulls (including a holotype, [2]). Some postcranial bones

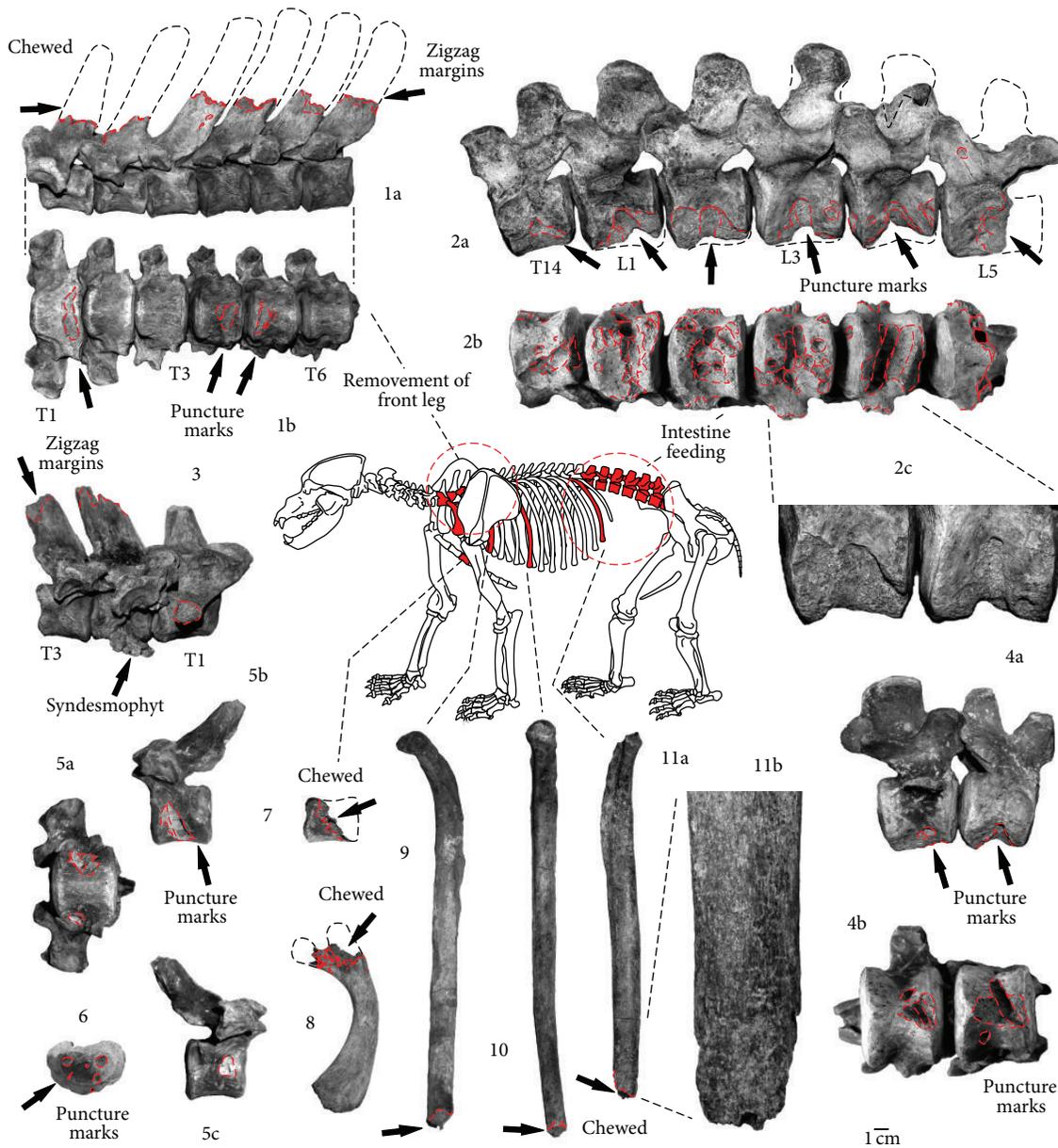


FIGURE 7: Cave bear bones of the small cave bears from the Bears' Passage of the Sophie's Cave (southern Germany) that have been chewed, bitten, and cracked by large predators (lions, hyenas, and wolves). 1–10 were from the Bear's Passage and 11 was from the Reindeer Hall (cf. Figure 1(e)). (1) Anterior thoracic vertebral column from a skeleton, with chewed dorsal spines and canine impact marks from a large predator (lion or hyena) on the sides of the ventral centre: (a) lateral, (b) ventral. (2) Distal thoracic to last lumbar vertebra from a single skeleton, with large scratch marks and round to oval canine impact marks from a large predator (lion or hyena), as a result of feeding on intestines and filet meat; (a) lateral, (b) ventral, (c) detail view of 6 mm wide bite scratches. (3) First three thoracic vertebrae from a single individual, with chewed dorsal spines and evidence of arthritis in the middle vertebra. (4) T14/L1 vertebrae from a single individual, with deep bite scratch marks from a large predator (lion or hyena): (a) lateral, (b) ventral. (5) Anterior thoracic vertebra with bite marks from a large predator (lion or hyena), (a) ventral, (b) lateral right, (c) lateral left. (6) Vertebra disc from a young individual, with several round to oval bite marks from a large predator (lion or hyena): cranial. (7) Sternal bone, half eaten: lateral. (8) First costa with chewed joints: lateral. (9) Costa, distally chewed: inner view. (10) Costa, distally chewed: inner view. (11) Costa, chewed at both ends: (a) inner view, (b) outer view with bite mark details (All from coll. Museum Castle Rabenstein).

have been compared, having similarly large proportions to those from the Sophie's and Große Teufels Caves where the bone sizes are closer to those of Scandinavian Arctic and Canadian Columbian wolf subspecies [54–58] than to those

of the smaller European wolves. They possibly belong to a specialized Late Pleistocene wolf ecomorph [55].

Coprolites (91 nearly complete and 160 fragments) were found at the end of the Bear's Passage that was blocked from

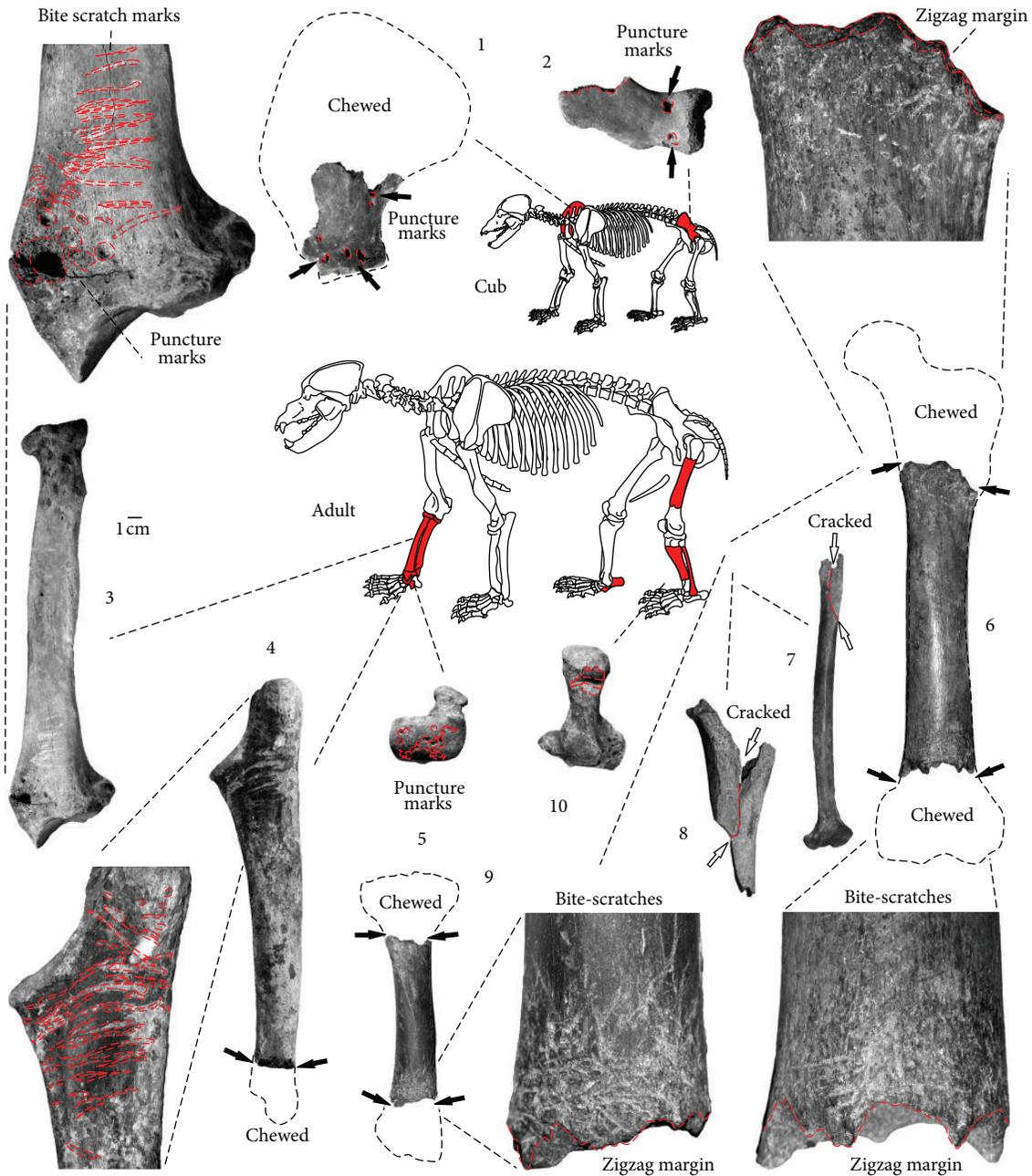


FIGURE 8: Cave bear bones of the small cave bears from the Bear's Passage of the Sophie's Cave (southern Germany) that have been chewed, bitten, and cracked by large predators (lions, hyenas, and wolves). (1) Scapula from a cub with smaller puncture marks, possibly from wolves: lateral inner view. (2) Pelvic ileum from a cub, with small to medium-sized puncture marks, possibly from wolves or hyenas: lateral outer view. (3) Radius with bite scratch marks and small puncture marks, possibly only from wolves: lateral inner view. (4) Ulna, distally chewed and with proximal bite scratch marks, possibly from wolves or hyenas: lateral inner view. (5) Scapholunatum with small puncture marks from wolves: dorsal. (6) Femur, both ends showing chewed joints with typical zigzag margins produced by wolves or hyenas: cranial. (7) Fibula with chewed and cracked proximal joint, cranial. The broken off bone fragment was also found in the Bear's Passage, proving scavenging on site. (8) Tibia shaft cracked by hyenas: lateral. Both parts were found in the Bear's Passage, again proving scavenging on site. (9) Tibia, with chewed joints at both ends showing zigzag margins, produced by wolves or hyenas: cranial. (10) Calcaneus with bite scratch marks produced by wolves or hyenas: caudal (All from coll. Museum Castle Rabenstein).

the Reindeer Hall prior to its use as a wolf den (Figure 5(a)). At this time the cave bears were unable to penetrate the cave system to their deep hibernation areas in the Millionary Hall (Figure 5(a)) and were therefore too close to today's

blocked entrance and within easy access of predators. About twelve of the coprolite pellets contain visible bone fragments, mainly of spongiosa bone material (Figures 11(1) and 11(3)–11(6)). Those are similar to spongiosa in cave bear bones,

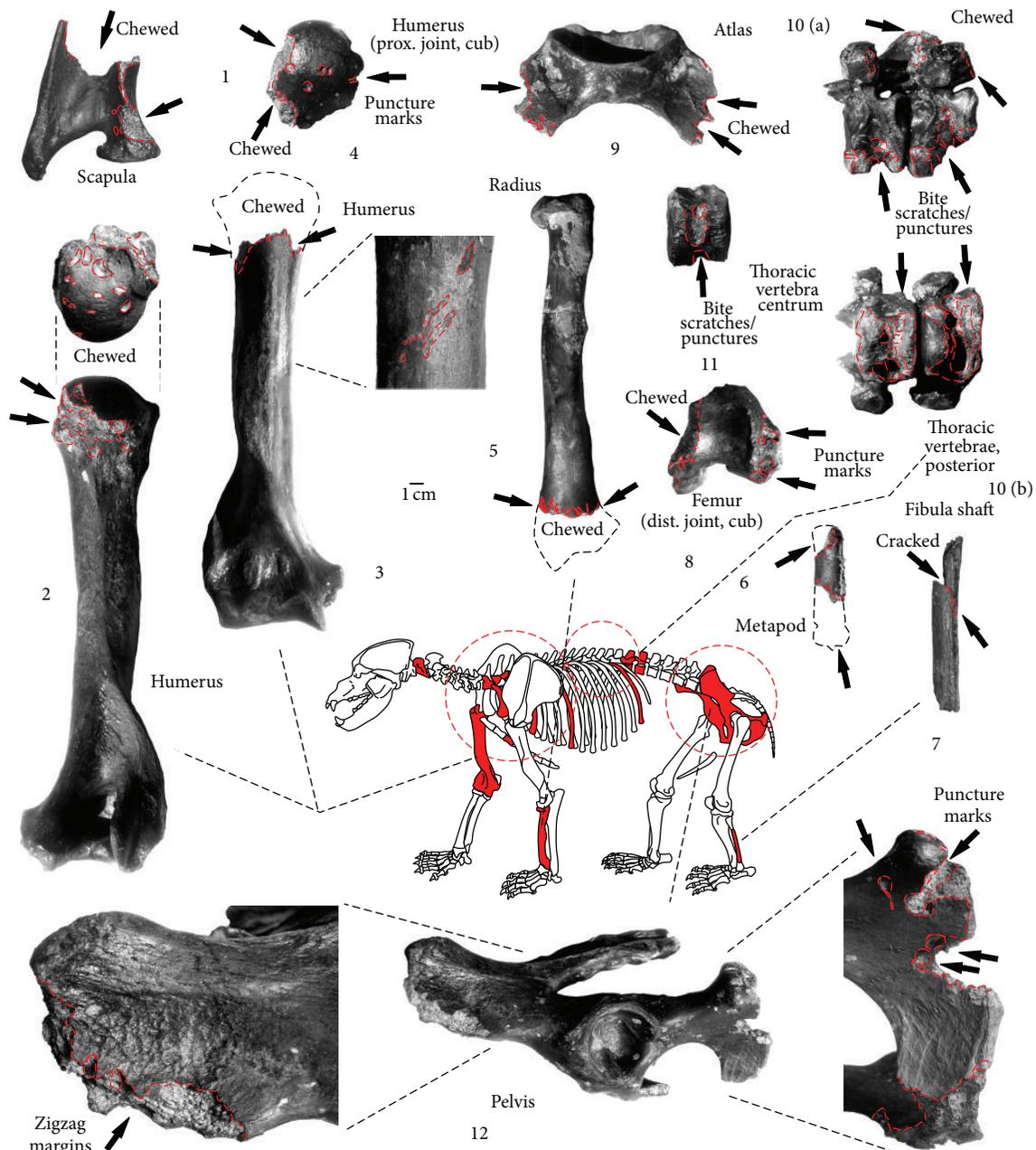


FIGURE 9: Cave bear bones of the small cave bears from the Reindeer Hall bonebed of Sophie's Cave (southern Germany) that have been chewed, bitten, and cracked by large predators (lions, hyenas, and wolves). (1) Scapula half eaten. (2) Humerus proximally chewed. (3) Humerus proximal joint eaten. (4) Proximal humerus joint with bite damages. (5) Radius distal joint eaten. (6) Metapodial chewed. (7) Fibula shaft, cracked. (8) Femur distal joint bite damaged. (9) Atlas laterally bite damaged. (10) Two posterior thoracic vertebrae with bite damages. (11) Thoracic vertebrae centrum with bite damage. (12) Pelvis, with puncture and bite scratch marks from a large hyena or lion and zigzag margins (all from coll. Museum Castle Rabenstein, left on place).

most probably from the vertebrae and pelvic bones. Few bone compacta are present, mainly resembling rib fragments found in the pellets or in the sediment (Figure 12). They are different from hyena coprolites in which more massive bone compacta fragments are generally preserved [59, 60]. The Sophie's Cave wolf faeces can also be distinguished from hyena pellets by their different shape and size. Hyenas formed larger aggregates (up to 5 cm in diameter; [32, 59, 60]), that had a more disc-like or larger drop-shape [59, 60]. Wolf excrements

instead are more elongated and slim with maximum diameter of 2.5 cm (Figure 11). Because of the large quantities of pellets and following comparisons with the faeces of modern wolves, a reasonably firm attribution to wolves can be made [61, 62].

**3.5. Partly Digested Cave Bear Bones.** The sieved smaller bone fragmentary material from the Bear's Passage yielded 360 bone fragments that must have passed through a carnivore's stomach. These bones and bone fragments show dissolution

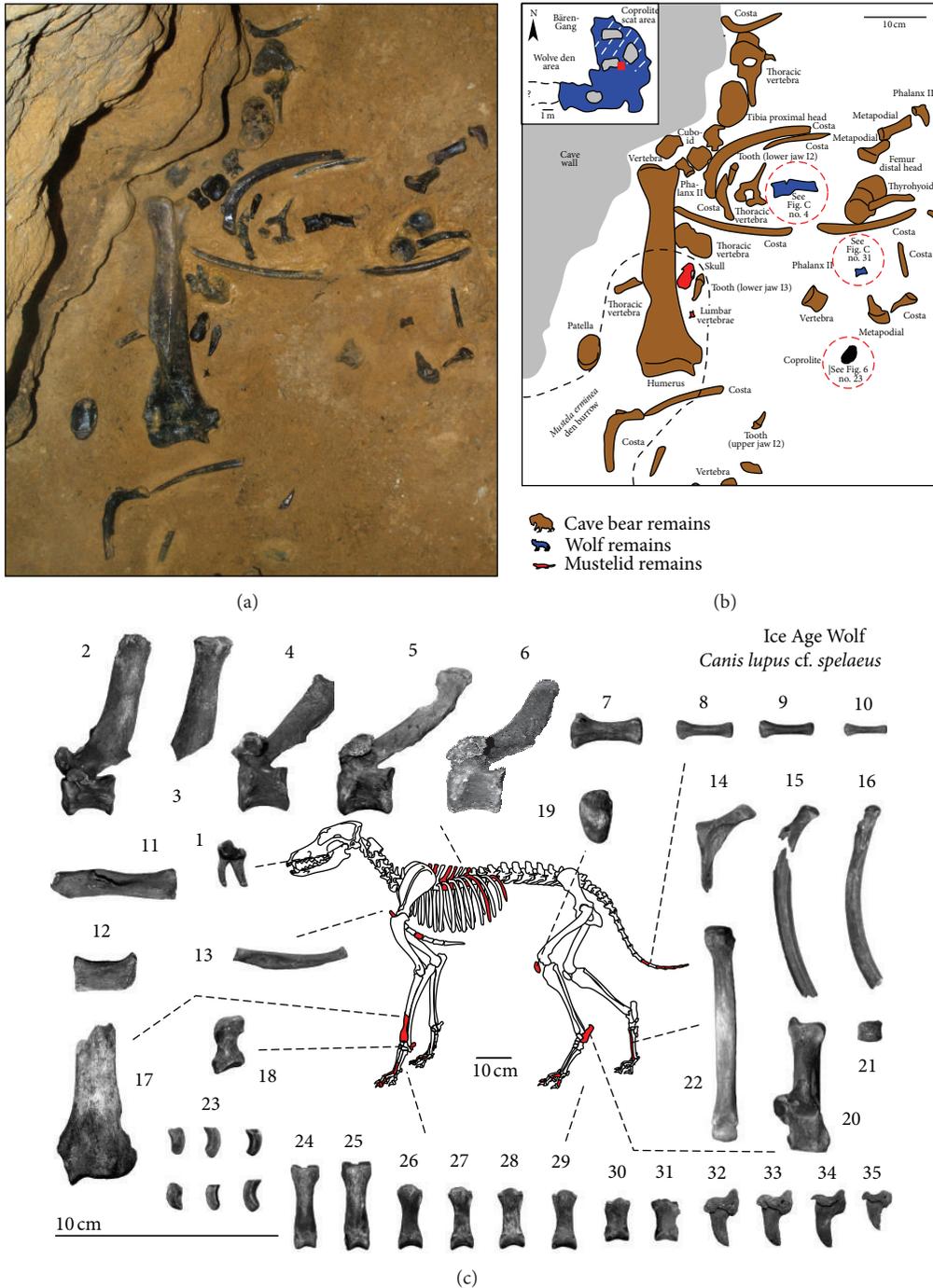


FIGURE 10: *Canis lupus cf. spelaeus* remains from adult animals, possibly from a single individual, from the Bear's Passage of the Sophie's Cave. (a) Bonebed with wolf and coprolite remains between cave bear bones. (b) Sketch of (a). (c) Bones: (1) right upper jaw M<sup>2</sup>. (2) First thoracic vertebra. (3) Anterior thoracic vertebra, dorsal spine. (4) Middle thoracic vertebra. (5) Posterior thoracic vertebra. (6) Upper caudal vertebra. (7) Middle caudal vertebra. (8) Middle caudal vertebra. (9) Distal caudal vertebra. (10) First sternal bone. (11) Middle sternal bone. (12) Last sternal bone. (13)–(15) Incomplete ribs. (16) Left distal radius. (17) Left pisiform. (18) Patella. (19) Left calcaneus. (20) Tarsal bone. (21) Left Mt IV. (22) Six sesamoids. (23)–(24) Phalanx I. (25)–(29) Phalanx II. (30)–(33) Phalanx III. (All in coll. Museum Castle Rabenstein).

structures such as the irregular surfaces on several phalanges and sesamoids (Figure 12, (1)–(9)), including stomach acid corrosion holes (Figure 12, (32)). These partly digested bones are compacta or spongiosa bone fragments from all parts of cave bear anatomies, although fragments of massive long

bones are relatively rare and only very small (Figure 12, (23)–(27)).

Most of the bone material that has dissolute surfaces cannot be clearly attributed to carnivores but the coincidence of finding damaged cave bear vertebral columns as well as their

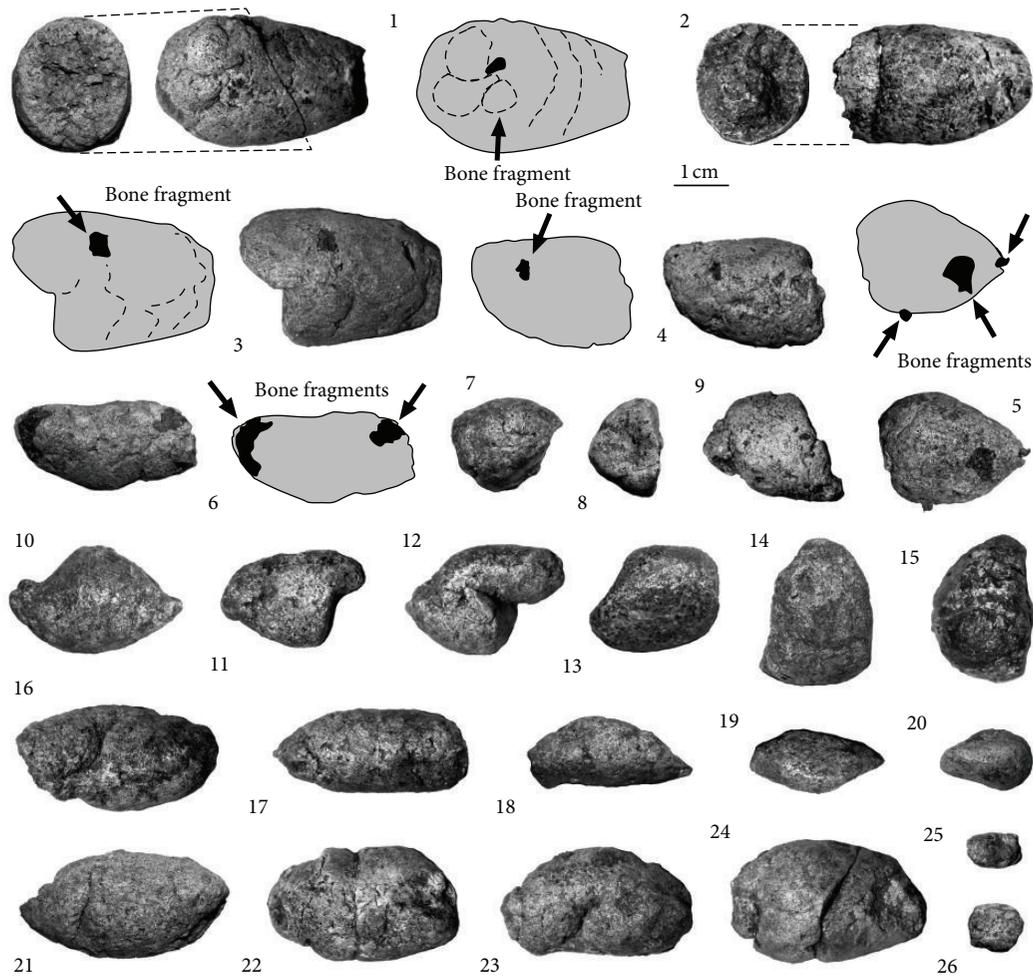


FIGURE 11: (1)–(26) Coprolites, some with cave bear bone fragments, all found in the Bear's Passage together with many single cave bear bone remains that have been partly chewed, cracked, or dissolved by stomach acid (all in coll. Museum Castle Rabenstein).

cracked and chewed bones and wolf coprolites in the same area makes it seem likely that these fragments have all originated from cave bears. Stronger evidence comes from five cave bear phalanges (three first and two second phalanges), two sesamoids, a thyrohyoid, and three vertebrae central fragments that are secure of cave bear origin (Figure 12, (1)–(13)). These coprolites which can be well distinguished with their elongated forms from those of hyena aggregate pellets [59] and bone fragments, together with the damaged bones, provide the first evidence in Europe suggesting scavenging by wolves within a cave. The small pieces of bone spongiosa and ribs in the coprolites all seem to be of only cave bear origin, and thus the pellets with bones, partly digested bones, and bones damaged by chewing found in the Bear's Passage of the Sophie's Cave must have ultimately been the result of wolves scavenging on cave bear carcasses (especially ribs, vertebral column, and pedal bones), and of the den marking behaviour exhibited by modern wolves [54, 61–63].

**3.6. Cave Bear Species and Subspecies in Europe and Sophie's Cave.** Four different cave bear species or subspecies from

the Late Pleistocene of Europe have recently been interpreted with the small alpine form *Ursus spelaeus ladinicus*, the middle mountainous region forms of the Early to early Late Pleistocene *Ursus spelaeus eremus*, *Ursus spelaeus spelaeus*, and the largest forms with *Ursus ingressus* at the final Late Pleistocene [18, 19, 64] (Figure 2). In the early to middle Late Pleistocene cave bears *U. spelaeus eremus/spelaeus* lived all over Central Europe [64, 65], until the middle Late Pleistocene, such as in the Sophie's Cave (Figure 3). With drastic climatic change to increasing glacial conditions [66], the latest Late Pleistocene larger cave bears *U. ingressus* (Figure 2) [64, 67] seem to have immigrated from the carpathians (interpretation herein) which is also present in Franconia, and the Sophie's Cave (Figures 2 and 3). The expanding Scandinavian and Alpine glaciers caused drastic climate and habitat changes all over Europe in the final Late Pleistocene around 22.000 BP with the maximum glaciation peak (Figure 2) [66]. The Early/Middle Late Pleistocene megafauna of the mammoth steppe low lands and even the final Late Pleistocene huge cave bear forms in the boreal forest mountains disappeared, finally, as herein discussed due to habitat change, and predation

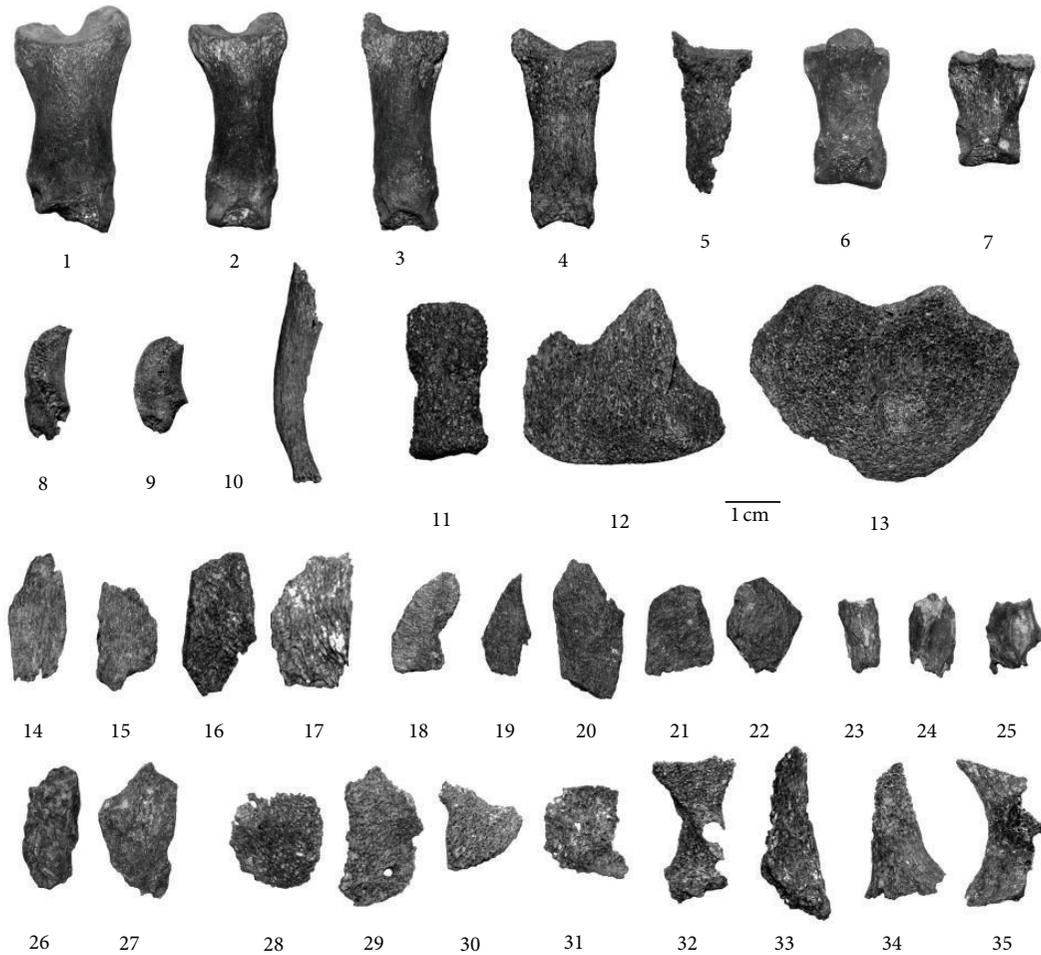


FIGURE 12: (1)–(35) Cave bear bones and fragments, partly digested and dissolved by stomach acid, all found all in the Bear’s Passage together with many faecal pellets and chewed cave bear bones. Paw bones: (1)–(5) Phalanx 1. (6)–(7) Phalanx 2. (8)–(9) Sesamoids Cranial bones. (10) Thyrohyoid; Thoracic bones. (11)–(13) Caudal and lumbar vertebra central fragments. (14)–(22) Costae fragments. (23)–(27) Unidentified bone fragments: bone compacta fragments. (28)–(31) Bone spongiosa fragments. (32)–(35) Unidentified fragments (all in coll. Museum Castle Rabenstein).

stress. The arctic “reduced reindeer fauna” took then over northern Central Europe (Figure 2) [68, 69].

**3.7. Cave Bear Predators and Scavengers.** It was generally suggested before that only “natural mortalities” occurred in those cave bear populations which were found in caves [70, 71]. First interpretations of carnivore impact on cave bear populations were discussed in a single European cave [72]. New research has demonstrated that cave bears indeed have been the main food source for these large Ice Age predators (lions, hyenas) in boreal forest environments [1–3], whereas newest nitrogen isotope analyses have additionally suggested lions to have fed at the end of the Late Pleistocene mainly on cave bear cubs at least [73]. This predation on cave bears is supported herein with further evidence from the German Sophie’s Cave (Figures 1(b)–1(e)). The impact of carnivores in this cave appears to have been quite high (18% of the cave bear bones have been damaged by carnivores) which needs to be taken into account in any studies on the life and death of European cave bears. They would have been at their

most vulnerable during winter hibernation and when raising young cubs (Figure 2) [1, 32, 74].

The Ice Age wolf in Europe *Canis lupus* cf. *spelaeus* is herein newly introduced as a “cave bear scavenger” and is not revised yet as lack of DNA studies, but its bone proportions are close to the Canadian timber wolf compared to skeletal material, and the Late Pleistocene wolf of Central Europe was a little larger than the modern European wolf. They possibly belong to a specialized Late Pleistocene wolf ecomorph [55]. It also appears that in the early to middle Late Pleistocene this large wolf existed all over Europe, which was then replaced directly within the maximum glaciation by the smaller wolf type, which finally disappeared with the reindeer fauna, replaced finally by the Holocene warm period European wolf *Canis lupus lupus*. Also the ecology of early to middle Late Pleistocene wolf within the mammoth steppe and boreal forests was quite unknown, also if those used caves as dens. Denning in wolves was reported in a first study in the Late Pleistocene of northern Italy [53], but similar as in Germany, most hyena “wolf den caves” overlap with “hyena

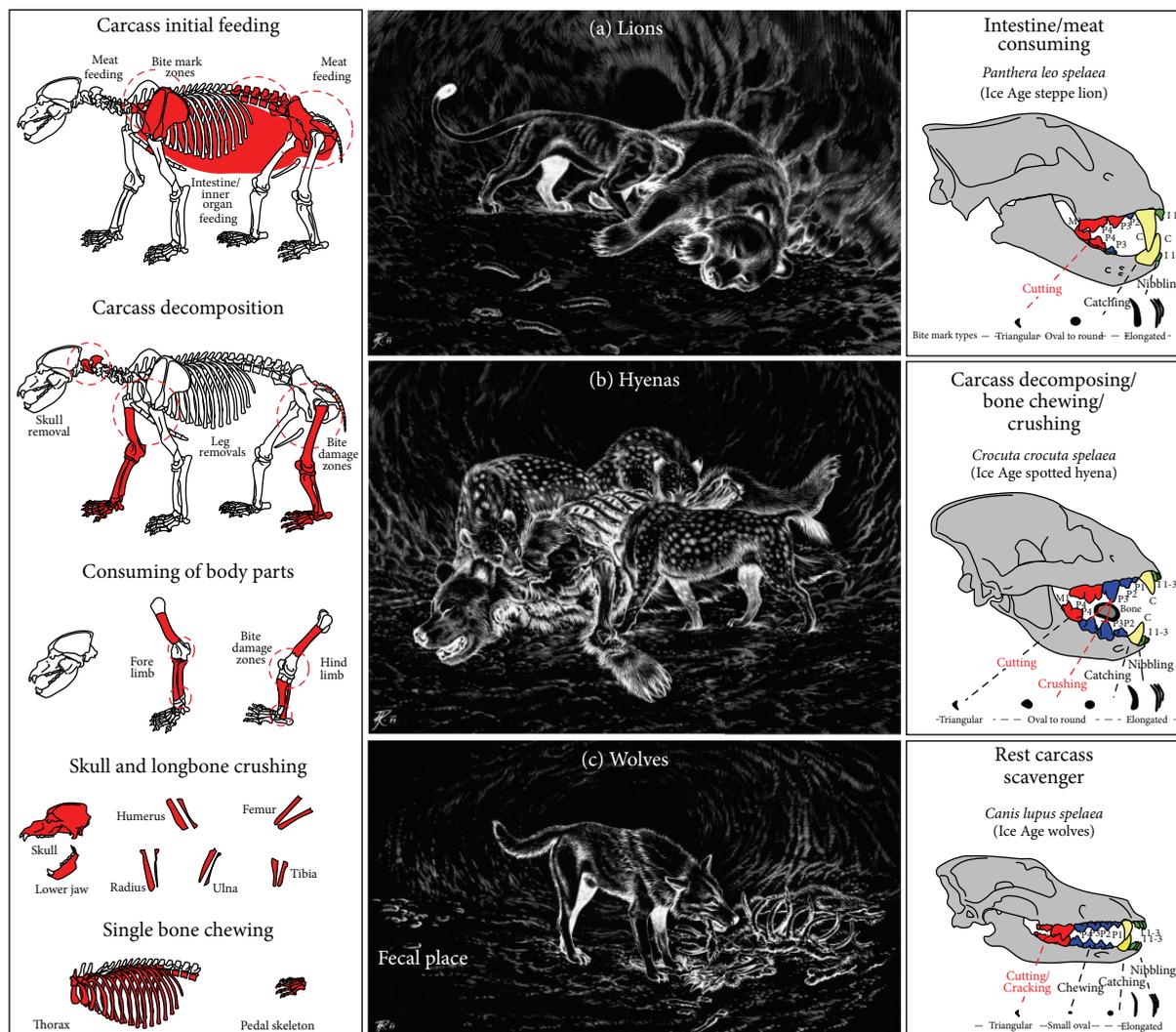
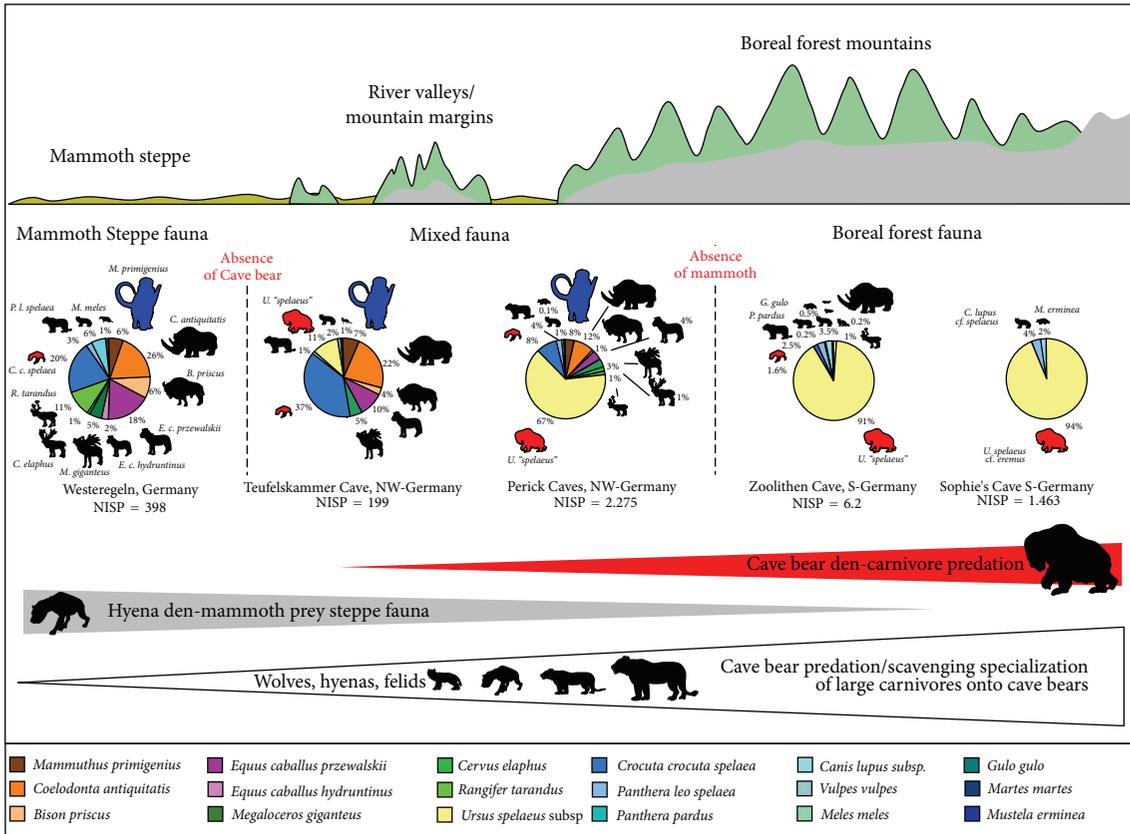


FIGURE 13: A picture story of the scavenging on cave bears by the three large Ice Age predators, and their differences in bite and jaw/tooth specializations for specific functions. (a) Ice Age steppe lion on its cave bear kill, consuming only the intestines and inner organs, and possibly some meat (e.g., tenderloins on the inner lumbar vertebral column) using its meat-cutting dentition (carcass initial feeding, possibly initial carcass decomposition). (b) Ice Age spotted hyenas destroying and damaging the cave bear carcass, including bone crushing with its bone crushing dentition (carcass initial feeding, decomposition, consuming of body parts, and skull and bone crushing). (c) Ice Age wolf consuming distal parts, soft ribs, and spongy parts of the pelvis and even the vertebrae, paws, and tail, that were left by other predators (single bone chewing). These wolves marked part of the Bear's Passage with their faeces, in which several cave bear bone fragments prove that they fed on cave bear carcasses and used the cave as their den ("cave imaging" illustrations by G. "Rinaldino" Teichmann; Graphics: PaleoLogic).

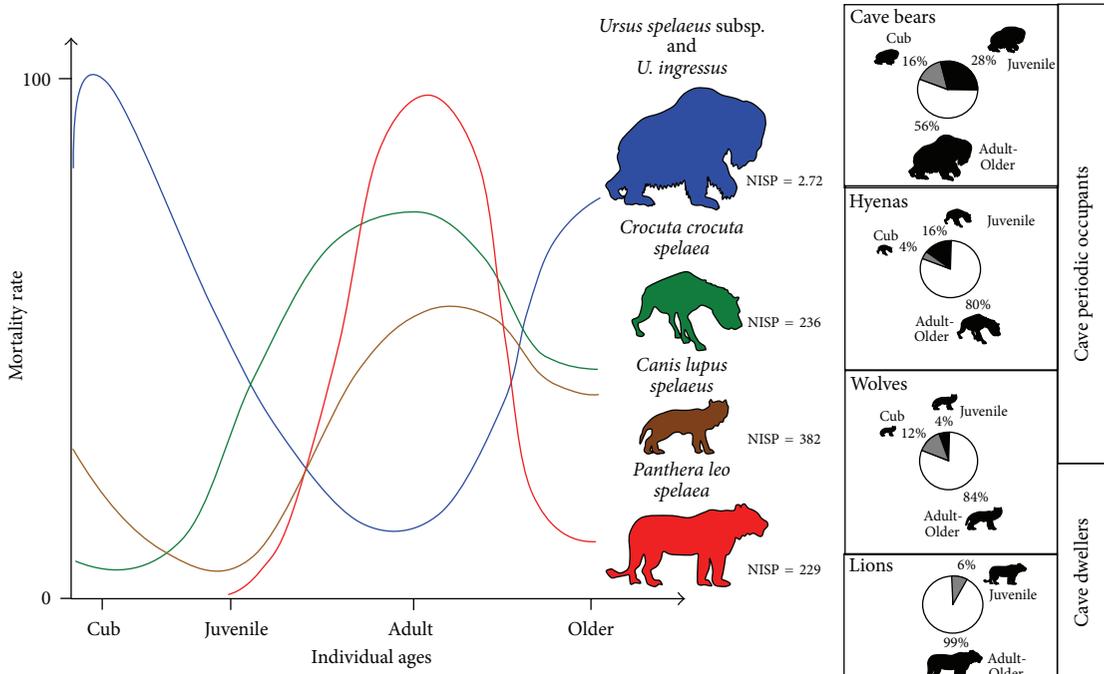
den sites," and the question still remains, if hyenas imported wolf carcass remains to their dens (in bone accumulations typically present), or if wolf bones in caves are simply results of their den use, and scavenging on wolf carcasses by hyenas? The taphonomy of wolves in "hyena den bone assemblages" remains unsolved. Extant wolf remains are not abundant in smaller caves, which are used by modern wolves as cub raising dens, and modern wolves do not import those amounts of carcass remains (even if it seems to be mainly reindeer) to caves (such as hyenas). At least rarely they only use those shelters for cub raising [56]. Until today, it is unsolved, if wolves used caves as dwellers, as dens, and prey storage or if their bone remains are results of battles with hyenas, lions,

and cave bears in caves in the Late Ice Age of Europe. The bone taphonomy situation is even more complex, as in lions, or hyenas.

New discoveries in the Sophie's Cave not far from the Zoolithen Cave, Bavaria, Germany (Figure 1(b)), presented herein, allow the first insights to the feeding habits in mountain regions and cave den use behaviour of Late Pleistocene wolves, which had to compete with two larger predators, lions and hyenas, which has no modern analogy. Obviously, in studied caves of Germany, most of the wolf bones were found at hyena dens, also partly at cave bear den caves presented herein with a first overview of the Franconian caves (Figure 1(b)). The largest unpublished amount of wolf



(a)



(b)

FIGURE 14: (a) Comparison of three main bone assemblage types from the mammoth steppe to those from mountainous Boreal forest Ice Age palaeoenvironments composed in northern and southern Germany. All herein studied Upper Franconian larger caves (Figure 1) seem to contain only the “Boreal Forest Fauna” bone assemblage such as analysed well for the Zoolithen and Sophie’s Caves. Carnivores adapted to specialize in feeding on cave bears in response to the absence of large mammoth steppe game fauna such as mammoths, rhinos, bison, and horses. (b) Mortality rates for cave bears, lions, and hyenas in the Zoolithen Cave as evidence of their use of the cave as a dwelling place or for other purposes only.

remains in this cave-rich region comes from the Zoolithen Cave, whose material is included in a preliminary study of this “large population” (about 400 bones). Other bones of large wolves can be reported after first “cave bear bone dump” studies in the Upper Franconia Große Teufels Cave (Figure 1(b)). At minimum, there are three caves of Upper Franconia (Zoolithen, Große Teufels, and Sophie’s Caves), which have both cave bear and hyena dens (Figure 1(b)). Those can be demonstrated to have larger amounts of wolf bones (Zoolithen Cave: 400, Große Teufels Cave: 50, Sophie’s Cave: 55 wolf bones). The Sophie’s Cave material is studied first in greater detail, which has not only wolf bones, but also, unique in Europe, wolf faecal pellets (not hyena, see hyena coprolite morphology in [59]), and even many bone fragments, and pedal bones from those faecal places of cave bears, which were partly digested, by wolves.

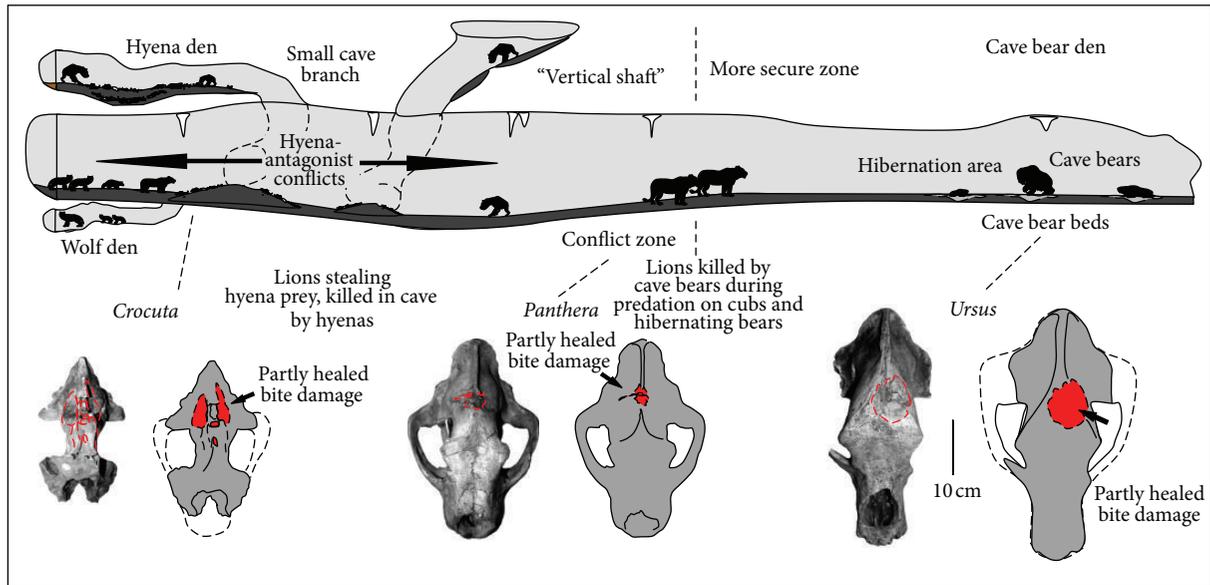
Ice Age steppe lions must have been good climbers and nocturnal hunters similar as their modern African relatives [75, 76]. They hunted and killed cave bears deep inside their caves, possibly while the bears were in hibernation, as has been clearly illustrated by the discovery of articulated lion skeletons amongst cave bear skeletons and their hibernation platforms 800 meters from the entrance of the Ursilor Cave in Romania [77]. Supporting evidence has also recently been found in the Zoolithen Cave [10] and many other caves of the Sauerland Karst in north-west Germany [47] as well as the famous Sloup Cave hyena and cave bear den in the Moravian Karst of the Czech Republic [46]. Newest nitrogen isotope studies also identified lions even as cave bear cub consumers in Europe [73].

Modern African spotted hyenas [75, 78, 79] and fossil Ice Age spotted hyenas are close related subspecies [80] and are poor climbers and seem to have mainly cleaned the caves of rotting carcasses, although operating in clans in the cave entrance areas they could also have easily killed cave bears themselves, and especially cave bear cubs [1–3]. At many of the German caves, including the Zoolithen Cave, Perick Caves, Balve Cave, and the Teufelskammer Cave in the Neander Valley they are thought to have been the main destroyers of cave bear carcasses and bones and to have specialized in feeding on cave bears in the mountainous boreal forest palaeoenvironments of the last Ice Age [1, 31, 52, 81–83]. Similar overlapping hyena den and cave bear den sites have been described from the Bohemian [60] and Moravian Karst, especially in the Sloup Cave [33] where hyenas in this mountainous region specialized in horse hunting [2], probably as a reaction to the absence of other megafauna prey or to their seasonal migrations. Horse hunting was also in the low lands important for hyena clans, demonstrated most recently at the German open air site Westeregeln [32]. Badly damaged cave bear bones indicate the importation of cave bear carcasses and single bones to open air dens such as the open air sites (close to mountain regions) at Bad Wildungen and Bottrop [82, 84].

**3.8. Lions as Cave Bear Killers.** All of the cave bear den caves studied in Germany contain only 1–3% of lion bones of *Panthera leo spelaea* as the only known large Late Pleistocene cold period felid of central Europe [85], of which none are from

cubs and those from juveniles or early adults are extremely rare [10, 46, 47, 60, 74, 86]. The highest rate of lion mortality in caves occurs at their peak reproductive age, as has been recently demonstrated for the largest known European steppe lion population in the Zoolithen Cave [10] (Figure 14(a)). Articulated lion skeletons have also been found between cave bear skeletons deep within the Ursilor Cave, as far as 800 metres from the entrance, these being the only large predator remains found so deep inside a cave bear cave [3]. Modern lions being good climbers and nocturnal hunters [75, 76], the Late Pleistocene lions appear to have been active in killing cave bears also in darkness deep in caves [10], probably largely during the winter when the bears were hibernating [10]. Whether the bears were killed by prides of lions or by individuals remains unclear, but a lion pride would probably be required for successful hunting of adult cave bears [10] and could have even successfully defended it against hyenas, such as well documented about the lion-hyena antagonism in Africa about megafauna prey [87–89]. The cave bear consuming of Late Pleistocene steppe lions was also proven recently with nitrogen isotopic analyses [73]. As with modern lions, the Ice Age steppe lions probably fed first of all on the intestines and inner organs of the bears (Figure 13(a)), leaving large canine tooth marks and scratches on the bones, especially on the soft spongiosa of vertebrae and long bone joints, as found in the cave bear bone material from the Sophie’s Cave (Figures 6–9). The bite damages on skulls of both, lions [90] and cave bears (Figure 15) seem to have resulted from their battles in the caves from intra- or interspecies fights.

**3.9. Hyenas as Cave Bear Cub Killers and Main Carcass Destroyers.** Ice Age spotted hyenas were cave dwellers similar to modern African spotted hyenas [75, 79, 91], whose Pleistocene subspecies sometimes occupied mainly only the entrance areas of caves or chambers which had vertical surface connections to longer horizontal caves [1, 2, 10, 92–94] (Figure 15(a)). They accumulated prey remains (hyena bone assemblages) in these areas during the Late Pleistocene (Figure 2(b)), as modern spotted hyenas cause bone assemblages less at birth such as at communal dens [95–99]. Whereas in the Zoolithen Cave the entrance area was only used periodically as a hyena den [2] (Figure 15(a)), in the Sophie’s Cave the hyenas appear to have been more permanent cave dwellers. A similar situation can be found in most of the European caves used as cave bear dens, in which the presence of hyenas can only be demonstrated indirectly by the damage on cave bear bones [1–3]. Hyenas are interpreted as having cleaned the caves of rotten carcasses, but they may also have operated in clans to kill cave bears (especially cubs) in the more easily accessible cave areas [2]. The Pleistocene cave bear hunt and feeding is unique in the history of hyenas, because modern ones do not overlap with bears anymore and hunt different migratory prey [78, 100, 101]. Only hyenas, with their jaws specialized for cracking bones [102] (Figure 13(b)) were capable of cracking all the massive long bones of cave bears [2, 3]. These fragments and incomplete bones were previously not collected or studied, resulting in a false picture of cave bear populations and “natural mortalities” in many



(a)



(b)

FIGURE 15: General Late Pleistocene model for the maximum of cave use and conflicts between all top predators, and cave bears with skull examples of the Zoolithen Cave (Upper Franconia, Figure 1) which model is also based on the Sophie’s Cave situation. (a) Skull damage as a result of predator and (b) cave bear fights (“cave imaging” illustrations by G. “Rinaldino” Teichmann; Graphics: PaleoLogic).

cave sites across Europe. Recent “bone damage stage” analyses have demonstrated hyenas to have been the main consumers of cave bear carcasses and destroyers of their bones, even outside the caves [82, 84]. This also indicates that the almost complete absence of articulated cave bear skeletons in Europe is mainly a result of carnivore activity rather than of trampling by bears as has been previously suggested [2, 3].

**3.10. Wolves as the Final Cave Bear Carcass Scavengers.** With the evidence from the Sophie’s Cave, wolves can be added at least at that site only as the third large predator to have consumed the rests of already scavenged cave bear remains, and possibly also to have killed cubs by hunting in packs, even within the caves. The carcasses must have been fed on first by the larger predators, which left massive impacts in the bone spongiosa, whereas the hyenas are the only that were able to crush the long bones into pieces [3]. Wolves only had a chance to feed on those by hyenas and lions left carcasses of grown up cave bears, whereas even foxes might have caused some bite scratch marks. The faecal pellets and partly digested cave bear bones from the wolf den area in the

Bear’s Passage of the Sophie’s Cave are the first clear signs that they may have fed on the European cave bears. Those wolf pellets are much different in shape as the ones of hyenas [59]. Similar to that in the Sophie’s Cave, where few wolf bone materials are recently available from the Early-Middle Late Pleistocene layers of the Bear’s Passage, in the Upper Franconian Zoolithen Cave, where a large wolf population is known to have existed (more than 400 bones) and where the entrance was easily accessible, smaller cave areas can be expected to have been used as cub raising dens by wolves. The wolf mortality rate at the Zoolithen Cave (which cannot yet be estimated at Sophie’s Cave) is very similar to that of hyenas (Figure 14(b)), indicating that they used the cave as a dwelling place and cub raising den. Sophie’s Cave has yielded few more wolf remains of wolf cubs in the material from the late Late Pleistocene layers, but also those are still too few for bone statistics. As with the lions and hyenas in the cave, the presence of wolves at least also indicates predation on cave bears (Figures 13(c) and 14(b)), and hence no “natural mortalities” can be expected in any European cave bear populations, as already mentioned [72]—this has only

been suggested without taking into account the possibility of predation by carnivores [70, 71].

During the Pleistocene wolves only used caves for cub-raising, as in the present day [53, 56, 58]. More mortality of their juveniles can therefore be expected outside, rather than inside, the caves. The Pleistocene wolves were present in caves in larger amounts of bone remains than known for modern wolves. Wolves may also have been killed during their predation activities by adult cave bears (see battles between brown bears/ice bears and wolves in North America: [103–107]), but their bone record seems to be complex and importation and killing by hyenas within the cave is an additional complicating factor. The only present-day comparison that can be made is with the antagonism between modern Canadian wolves and black bears (also hibernating in caves), which shows that both can be killed and scavenged by the other, especially in the case of weak animals or cubs [108].

In the Sophie's Cave the absence of a hyena den allowed wolves to occupy the Bear's Passage, and from its stratigraphical record this appears to have occurred during the final stages of the cave's use as a den by cave bears, when the connection between the Bear's Passage and the deeper hibernation areas of the Reindeer Hall and Millionary Hall was blocked. At the far end of the Bear's Passage a tunnel-like branch of the cave that was at least a few tens of metres deep provided a perfectly protected den for the wolves (Figures 5(b), 10(a), and 10(b)).

**3.11. Cave Bear Habitats and Dwarfism as a Result of the Absence of Hyenas.** The palaeobiogeography of cave bears is restricted to mountainous boreal forest regions and their river valleys (Figures 2 and 14(a)). The cave bear was not an element of the mammoth steppe fauna and inhabited only the mountainous regions of central Europe, with some smaller forms developing in the alpine regions (the Alps, and the Carpathians [51]). An explanation was given for those dwarf cave bears as result of insular effect in the alpine mountains or higher elevations, where hyenas and lions were absent clearly above 1.600 m a.s.l. The lack of the top predators, whose highest elevated remains were found in the Swiss Wildkirchli Cave near Appenzell (unpublished material), was discussed to be at least another reason [1] besides worse feeding conditions for small alpine cave bear forms. The only predators in those higher elevated mountains were the leopards and lions. It seems that cave bears might have migrated to Europe and retreated east-west several times, over the Carpathians and into the Caucasus regions (Figure 2), where cave bear studies in detail still are lacking. With the temperature drop starting around 26.000 BP (LMG; [21]) the migrations of the three recently identified Late Pleistocene cave bear subspecies (*U. spelaeus spelaeus*, *U. spelaeus eremus*, and *U. spelaeus ladanicus*, [21]) seem to have been replaced by the last and largest giant cave bears (*U. ingressus*), which are also represented in the youngest Late Pleistocene strata of the Sophie's Cave (Figure 2). At least in some regions, such as the Swabian Alb, it is already discussed that both cave bear forms of *Ursus spelaeus* subsp. and *Ursus ingressus* used the region and its caves parallel without mixing in the genes [19]. Also there finally only the large

*U. ingressus* survived as latest species between about 32.000 and 25.000 BP. These giant bears seem to have become extinct not later as in the maximum cold period around 24.000 BP [21], when the Scandinavian glaciers reached Hamburg and Berlin in northern Germany (Figure 2). The climatic changes of the two interstadials within the Late Pleistocene, and as mentioned by [19] especially in the LMG, seem to have been a main driver of the exchanges and cave bear evolution. The theory of predation stress by the three cave bear killers and scavengers of Eurasia, the lions, hyenas, and wolves is more and more included in studies. These predators fought not only with cave bears but also between themselves, and not only within the caves (Figures 14 and 15) [1]. Their interspecific and intraspecific fights resulted in the many instances of cranial damage [2, 10, 46], which were previously believed to have been the result of hunting by Neanderthals [109]. Whether the herbivorous cave bears were ever hunted by Neanderthals still remains unproven, whereas does any hunting of the largest predators of the Ice Age [47], which all would have been an extremely dangerous pursuit.

**3.12. Cave Bear Migration, Extinction-Climate, Vegetation, and Predation Stress.** Cave bears of *Ursus spelaeus* subsp. and *Ursus ingressus* were clearly mountain and boreal forest inhabitants, and their bones are abundant in many caves. Their remains are extremely rare in the mammoth steppe low lands (less than 0.1% of the megafauna bone remains), documented in Germany and Czech Republic [31, 81, 82, 84].

Cave entrances of larger cave bear den systems were often overlapping hyena [83, 92] and Middle to Late Palaeolithic (Neanderthal to Epipalaeolithic) camp sites. The extinction of cave bears cannot be attributed due to human hunt pressure at all, because there is the single cave in the Swabian Alb that demonstrated at least the carcass use and hunt, both at the latest large *U. ingressus* cave bears by modern Pleistocene humans of the Gravettian age [19].

The last cave bears of Europe appeared during the Aurignacian-Gravettian (and even before) with the species *Ursus ingressus* and seem to have replaced the older forms quite late, whereas both seem to have coexisted in the Middle Late Pleistocene already using the same cave-rich regions, such as the Swabian Alb [19]. *Ursus ingressus* remained as the only cave bear for at least circa 2.000 years after the last appearance of the classical cave bear *Ursus spelaeus* subsp. in the Swabian Alb Ach Valley. The final appearance of cave bear (*Ursus ingressus*) is dated back to 25,560 ± 130 BP [19]. Also in Sophie's Cave in the stratigraphy a "replacement" can be observed very well at the moment without absolute bone dating. The last cave bears, which might have migrated from Asia and the middle mountainous boreal forest, became extinct within the LMG (late Late Pleistocene: [19, 20]) when the climate already started to become cooler with its peak in the last maximum glaciation (about 24.000 BP).

After the *U. ingressus* dentition with multiple coned and enlarged crowns [26, 51] those had well developed herbivorous adapted jaws. It must be expected that those lived in the middle mountainous regions, where at colder periods an alpine flora was present, including blueberry-rich vegetation. Compared to modern brown bear populations in

the Slovakian Carpathians counting about 600–800 brown bears in an area of 12.500 km<sup>2</sup> and estimated European total amount of 18.000 brown bears [110] it must be expected that the amount of cave bears, for example, in Upper Franconia, was much higher as believed. In this area there are about one Million cave bear bones (from Late Pleistocene) only estimated yet using the most bone-rich caves: Sophie's Cave, Zoolithen Cave, Geisloch Cave, Große Teufels Cave, and some others (cf. Figure 1). There is no satisfying study that deals with such estimations of cave bear populations yet, but clearly the Late Pleistocene herbivorous cave bears were boreal forest inhabitants, whose remains are found to be extremely rare in the mammoth steppe low lands or river valleys in Germany [81, 82, 84, 111]. In Germany, the cave bear den regions correlate with the cave-rich mountainous regions such as the Sauerland Karst, Harz Mountain, Upper Franconia, and Swabian Karst [1]. The large amounts indicate cave bears to have occupied mainly those forests, where mammoth steppe megafauna only migrated seasonally within the valleys, but where reindeer herds are expected to have stayed in summer times [69]. The main food source for lions and hyenas must have been reindeers and cave bears, whereas red deer and smaller prey must be expected to have been hunted by wolf packs. The predation on reindeers and cave bear cubs before the last maximum glaciation [73] supports the theory that lions were choosing also in those forests cave bears as preys.

#### 4. Conclusions

In the Upper Franconian Alb mountains of Bavaria, South Germany, during the Pliocene this landscape was a plateau (elevation 450 a.s.l.). Pliocene and Early Pleistocene phreatic waters caused horizontal underground cave systems in massive Jurassic sponge-reef limestone dolomites. Today those are 1–3° rotated, as a result of Mid-Pleistocene tectonics. The Franconian valleys cut into the plateau during the Mid-Pleistocene, whereas oldest marten tracks in Sophie's Cave demonstrate the first cave use by small carnivores, which used small cavities to enter the cave. Within this time the cave was filled up only in the anterior cave parts (valley-side) massively by a first river terrace (Sequence 1, elevation 415–420 a.s.l.), coarsening up sequence which was covered by an undated speleothem layer. Further lowering of the terraces of the Wiesent and adjacent valleys (Sophie's Cave, Ahorn Valley) caused then further floods, but also removal of most of the Mid-Pleistocene sediments in the anterior cave area. At the end of the Mid-Pleistocene the Ahorn-Valley was half of its today depth eroded, and a first entrance was accessible starting during the Early Late Pleistocene. From there, first small cave bear subspecies (*Ursus spelaeus* cf. *eremus*) dating into the Early Late Pleistocene were able to penetrate as deep as possible for hibernation into the Sophie's Cave until the Millionary Hall. There, about eight hibernation nests are still preserved, but also some skulls and bones and even a partly articulated skeleton. The tooth morphology of the cave bears from the first "hibernation cave den use" and lower stratigraphic levels (Millionary Hall, Reindeer Hall, and Bear's Passage) by cave bears dates into

the early Late Pleistocene. Those cave bears were scavenged deep in the cave by hyenas, lions, and probably wolves. In the Reindeer Hall the new excavated bonebed includes articulated vertebral columns, and many bones with bite damages, indicating scavenging of their carcasses directly in their hibernation areas. During the Early/Middle Late Pleistocene boundary, the part between the Bear's Passage and Reindeer Hall was blocked by a large ceiling block, when also a first speleothem genesis created today's larger speleothems (small warm interstadial). The middle Late Pleistocene cave bears used then only the Bear's Passage as their den. Here massive scavenging on cave bears is documented again; unique are several vertebral columns with bite impacts of large hyena/lion canines, indicating the intestine feeding, possibly first. The former cave bear den entrance then was also blocked somehow at the boundary Middle/Late Late Pleistocene. During this period, the river terrace lowered first, but then the river valley was further filled up, such as marginal caves. The Sophie's Cave was flooded again and was filled on a lower elevation then again with a new terrace sequence of latest Late Pleistocene in age (elevation 425–420 a.s.l.). Dating of the layers comes from the final huge cave bear species *Ursus ingressus*, whose remains were found mainly in other cave areas. The river valley erosion opened at that time is today's entrance. Cave bears came from another direction and were able only to penetrate over the Ahornloch Hall to the Sand Chamber in its maximum. The final large cave bears used another cave area at the end, whereas their bones were finally transported during flood events of the Pre-Ailsbach into deeper or further cave areas. Most material was washed into the Bear's Catacombs, but very few were transported into the Reindeer Hall. Those younger *U. ingressus* remains overlay the older smaller *U. spelaeus* subsp. forms. The large portal invited also hyenas to use the anterior cave area as a den, which imported few woolly rhinoceros bones, Przewalski horse remains, and reindeer. Also wolves are still present in those younger layers. Again many cave bear bones have large carnivore bite damages, whereas a hyena jaw and subadult lion jaw/phalanxes are the few direct proof of their presence. After the disappearance of the "boreal forest megafauna," during the maximum glaciation, it seems, modern humans of the Late Magdalénian/Epipalaeolithics used only one difficult to reach room, the Reindeer Hall as sanctuary. More than 100 dropped reindeer antlers, selected male ones, a skull with antlers, might possibly represent a shamanic sanctuary of "reindeer hunters," reflecting the change from cave art to antler depots in rituals to their most important prey animal. The cave sanctuary correlates to a close related Late Magdalénian camp site of the Rennerfels Abri of the Ahorn Valley. Finally, already in the Late Magdalénian, the valley had been eroded on 380 a.s.l. close to today's elevation (375 m a.s.l.).

The Sophie's Cave is a key locality for regional understanding of landscape development of the Franconian cave landscape, accessibility of caves for carnivores and cave bears, and complex taphonomy in caves with flood and carnivore impact. It has demonstrated the first "Early Late Pleistocene wolf den" with intensive faecal places and first prove for feeding on cave bear carcasses by the first European record

of half digested cave bear bones found within the faecal areas in the cave. It demonstrates that wolves seem to have used this cave not as a cub raising den, but they were cave dwellers, which fed on cave bear carcasses, similar (but less) as hyenas and more such as lions. The abundant faeces seem to play a role in the “orientation” for trail tracking similar as in modern wolves, and less as den marking. The high abundance in a limited area of the Bear’s Passage might result of periodical short-term den use of smaller cave areas. Wolves were scavenging on the bears, so they hibernated and died there, however, and therefore a simultaneous use as wolf and cave bear den cannot be expected. Remains of a skeleton of at least one high adult wolf also might result in a battle within the cave with the bears, the same as in the lion taphonomic record.

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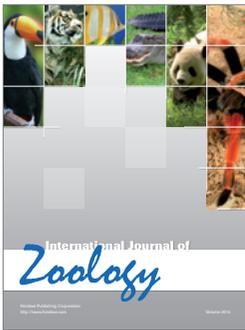
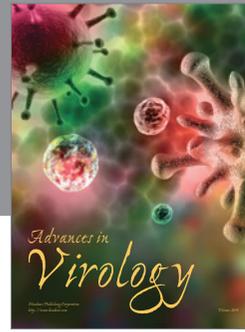
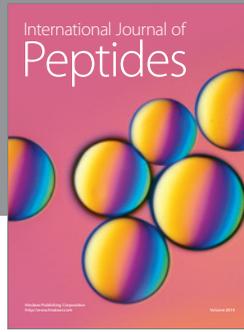
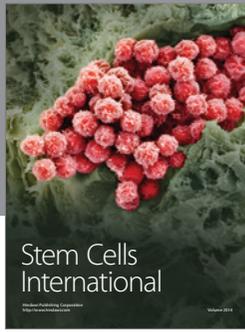
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