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Cajus G. Diedrich

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PLEISTOCENE *PANTHERA LEO SPELAEA* (GOLDFUSS 1810) REMAINS FROM THE BALVE CAVE (NW GERMANY) – A CAVE BEAR, HYENA DEN AND MIDDLE PALAEOLITHIC HUMAN CAVE – AND REVIEW OF THE SAUERLAND KARST LION CAVE SITES

Cajus G. DIEDRICH [1]

ABSTRACT

Pleistocene remains of *Panthera leo spelaea* (Goldfuss 1810) from Balve Cave (Sauerland Karst, NW-Germany), one of the most famous Middle Palaeolithic Neandertalian cave sites in Europe, and also a hyena and cave bear den, belong to the most important felid sites of the Sauerland Karst. The stratigraphy, macrofaunal assemblages and Palaeolithic stone artefacts range from the final Saalian (late Middle Pleistocene, Acheulean) over the Middle Palaeolithic (Micoquian/Mousterian), and to the final Palaeolithic (Magdalénien) of the Weichselian (Upper Pleistocene). Most lion bones from Balve Cave can be identified as early to middle Upper Pleistocene in age. From this cave, a relatively large amount of hyena remains, and many chewed, and punctured herbivorous and carnivorous bones, especially those of woolly rhinoceros, indicate periodic den use of *Crocuta crocuta spelaea*. In addition to those of the Balve Cave, nearly all lion remains in the Sauerland Karst caves were found in hyena den bone assemblages, except those described here material from the Keppler Cave cave bear den. Late Pleistocene spotted hyenas imported most probably *Panthera leo spelaea* body parts, or scavenged on lion carcasses in caves, a suggestion which is supported by comparisons with other cave sites in the Sauerland Karst. The complex taphonomic situation of lion remains in hyena den bone assemblages and cave bear dens seem to have resulted from antagonistic hyena-lion conflicts and cave bear hunting by lions in caves, in which all cases lions may sometimes have been killed and finally consumed by hyenas. The lion remains, and not only in the Balve Cave seem to have been selected, as suggested by cranial and distal limb bone overrepresentations, which consist of 99 % of grown ups and with 58 % remains of dominantly females. Such limbs, and especially the pedal bone dominance, is not a criterion for "human hunt and fur import", on the contrary, at hyena dens all prey remains are overrepresented by distal leg remains, a fact also very well known in the case of horse remains. The only articulated lion cub skeleton remain in the Sauerland Karst from the Wilhelms Cave might indicate a hyena kill that seems to be imported into the much frequented cub raising hyena den site.

Keywords: Lion *Panthera leo spelaea* (Goldfuss 1810), Balve Cave, north-western Germany, Sauerland Karst Mountains, cave bear/hyena den, Middle Palaeolithic human site, Upper Pleistocene

RÉSUMÉ

RESTES PLÉISTOCÈNES DE *PANTHERA LEO SPELAEA* (GOLDFUSS 1810) DE LA GROTTE DE BALVE (NO DE L'ALLEMAGNE) – UNE GROTTE À OURS DES CAVERNES, UNE TANIÈRE DE HYÈNE ET UN HABITAT DU PALÉOLITHIQUE MOYEN – ET RÉVISION DES SITES À LIONS DES GROTTES DU KARST DU SAUERLAND

Les restes pléistocènes de *Panthera leo spelaea* (Goldfuss 1810) de la grotte de Balve (karst de Sauerland, NO de l'Allemagne), l'un des sites néandertaliens en grotte les plus célèbres d'Europe, également tanière de hyènes et repaire d'ours des cavernes, proviennent de la plus importante des localités à félidés du karst du Sauerland. La stratigraphie, les assemblages de macrofaune et d'artéfacts du Paléolithique s'étalent de la fin du Saalien (fin du Pléistocène moyen, Acheuléen) au Weichsélien (Pléistocène supérieur), ces derniers incluant du Micoquien, du Paléolithique moyen (Moustérien) et du Paléolithique supérieur (Magdalénien). La plupart des os de lion de la grotte de Balve peuvent être identifiés comme étant du début et du milieu du Pléistocène supérieur. Dans cette grotte, une relativement grande quantité des os d'herbivores et de carnivores importés par des hyènes sont mâchés ou percés, en particulier ceux de rhinocéros laineux, indiquant que la grotte a été utilisée en tanière de façon périodique par *Crocuta crocuta spelaea*. En plus de ceux de la grotte de Balve, presque tous les restes de lion des grottes du karst du Sauerland ont été trouvés dans des assemblages de tanières de hyène, à l'exception du matériel décrit ici provenant de la grotte Keppler, un repaire d'ours des cavernes. Les hyènes tachetées du Pléistocène supérieur ont probablement importé des parties du corps de *Panthera leo spelaea* ou les ont récupérées sur des carcasses de lions dans les cavernes, ce qui est soutenu par des comparaisons avec d'autres grottes du karst du Sauerland. La situation taphonomique complexe des os de lion au sein des assemblages de tanières de hyène et de repaires d'ours des cavernes semble avoir résulté de conflits antagonistes entre hyènes et lions, et de la chasse des ours des cavernes par les lions dans des grottes, dans lesquelles les lions pourraient avoir parfois été tués et finalement consommés par les hyènes. Les restes de lions, mais pas seulement ceux de la grotte de Balve, semblent être sélectionnés, si on se réfère à la surreprésentation des os crâniens et des membres distaux, qui représentent 99 % d'adultes avec 58 % de restes de femelles dominantes. Ce fait, et en particulier la dominance des os du pied, n'est pas un critère indiquant la «chasse par l'homme et l'importation de fourrure», au contraire, dans toutes les tanières de hyènes, les restes de proies sont toujours surreprésentés par les restes des extrémités distales de membres, fait également bien connu pour les restes des chevaux. Le seul squelette articulé de lion immature connu dans le karst du Sauerland, dans la grotte Wilhelms, pourrait refléter une mise à mort de hyène et semble avoir été importé dans une tanière très fréquentée.

Mots-clés: Lion *Panthera leo spelaea* (Goldfuss 1810), Grotte de Balve, nord-ouest de l'Allemagne, montagnes karstiques du Sauerland, tanière de hyènes, repaire d'ours des cavernes, site du Paléolithique moyen, Pléistocène supérieur

[1] Petra Bezruce 96, CZ-26751 Zdice. *Courriel:* cdiedri@gmx.net

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1 – INTRODUCTION

Historically collected in caves, late Pleistocene bones, which were not often identified as lion bones, have been rediscovered from the Sauerland Karst cave and bone-rich region of north-western Germany, including the here focussed Balve Cave. These bones were found during many pioneer cave excavations during the 19th century (Virchow, 1870; von Dücker, 1870; von Dechen, 1871, 1879; Kremer, 1873; Schaaffhausen, 1875; Zygowski, 1988; Ahrweiler, 1995; fig. 1A-B).

The horizontal and large, but only 90 m long Balve Cave (elevation 230 m, fig. 1C) splits after 54 m into two branches: the Virchow and the Dechen branches, named after their excavators (fig. 1D). With its 11 m high and 18 m wide portal (fig. 1E), it is easily visible from the Hönnetal (Hönne Valley). At the beginning of the 19th century, the Balve Cave began to be intensively excavated by farmers for bones to use those as phosphatic agents. During that time, the uppermost speleothem layer, which is still today attached 4-5 m above the ground level to the cave walls, and the upper 1-2 meters of sediment of the upper "culture layers" were completely removed. First excavations concerning archaeology and faunal remains were made in 1843/44 (Bahnschulte, 1940). After this, Virchow (1870) and von Dechen (1871) excavated and described new finds from different areas of the cave. Although Kramer (von Dechen, 1879) and von Dücker (1870) also excavated in the cave, the largest historical scientific explorations were made by Bahnschulte (1940). He worked with the use of systematic trenches, which have produced the most important stratigraphic information (fig. 2). Finally, Günther (1964) excavated in 1959 close to the old trenches of Bahnschulte.

The Balve Cave is now one of the most famous caves in the Sauerland Karst of northern Germany (Brandt, 1939), but also a well-known archaeological locality in Europe. It has a combination of animal and human use over a period of more than 120,000 years and contains both, a large amount of artefacts (about 53,000), and bones (about 2,000) from several layers (Günther, 1988). The cave became famous early, because of its rich and large amount of Lower and Middle Palaeolithic (Acheulean, Mousterian, Micoquian) lithic artefacts, mainly made of regional black lydite and few imported quartzite or nordic flintstone (Kremer, 1873; Bahnschulte, 1938, 1940; Beck, 1975), as well as several bone artefacts that were found and repeatedly studied (Andrée, 1924, 1928; Brandt, 1939; Günther, 1964, 1988; Bosinski, 1984; Järis, 1992, 1993). A horse engraving from the Aurignacian period is the only important art find (Andrée, 1930).

Micromammals were already sieved in the 19th century and listed by Farwick (1870), von der Marck (1872) and Nehring (1879a, 1879b, 1880, 1883), but a modern stratigraphy-related and palaeoclimatologic micromammal analysis is missing. The macrofauna was generally only mentioned or listed without a good stratigraphic context, detailed species or subspecies names or quantitative analyses (Virchow, 1870, 1879; von Dücker, 1870; von Dechen, 1871, 1879, 1884; Kremer, 1873; Wollemann, 1887). At least Pohlig (1888) described woolly mammoth *Mammuthus primigenius* remains, but also not in detail, and not with a taphonomic study about hyena bite marks on those bones, or with a discussion to its possible hyena prey origin, which was later proven for some chewed and bite damaged bones (Diedrich, 2011d). A rare musk ox *Ovibos moschatus* skull (Andrée, 1933) was reported, and is now preserved in the small regional Balve Museum. *Hippopotamus amphibius* was described only briefly (Wollemann, 1887), which indicates the presence of interglacial (Eemian) sediments and fauna. The Pleistocene macrofauna was generally not studied and only listed by non-palaeontologists (Bahnschulte, 1940; Günther, 1988). This also results of the artefact and bone spreading in many collections (see Material and methods) and of problematic stratigraphic records. Hence, it was generally thought all to be "human bone importation" (Andrée, 1928; Günther, 1964, 1988). Only cave bear remains were mentioned as being the non-imported faunal remains of a cave bear den site (Bahnschulte, 1940).

Thirteen cave sites in the Sauerland Karst and five open air sites are known in Westphalia to have provided Upper Pleistocene *Panthera leo spelaea* (Goldfuss 1810) bone material (fig. 1A-B; Diedrich, 2009d) from Perick Caves hyena and cave bear den including the only preserved complete skull of the Sauerland Karst caves (60 bones; Diedrich, 2009a), Bilstein Caves cave bear den (30 bones; Diedrich, 2009d). The Balve Cave is also one of the few north-western German caves with a higher amount of lion remains as described herein. In this study, 48 lion bones from Balve Cave, and 35 bones from Keppler Cave cave bear den are added in a review, such as a few more remains from the Grürmanns Cave hyena den, Johannes Cave hyena den, Kreuz Cave, Martins Cave cave bear and hyena den, Teufelskammer Cave hyena den (Diedrich, 2011b), and Wilhelms Cave hyena den (fig. 1B). This lion material described herein and its taphonomic context in hyena dens and cave bear dens is of importance for the palaeobiological understanding of late Pleistocene lions and their antagonism to the last Ice Age spotted hyenas of Europe, cave bear hunt by predators (hyenas/lions; Diedrich, 2011e), and the taphonomy of lion bones in caves in general (cf. Diedrich, 2009a, 2009b). The material especially from the Balve Cave will be discussed in its "non-human context", whereas the former discussion about "importation of carnivores" by human hunters to their camp sites will be critically discussed with the material from a "human cave site" and "non-human cave sites" of the Sauerland caves.

2 - GEOLOGY AND DATING

The studied Sauerland Caves are all dated from the early to middle Upper Pleistocene by the megafauna assemblages (hyena bone accumulations, cave bear den bone accumulations), and cave bear tooth morphologies at the Perick, Martins, Grürmanns, Balve, Bilstein,

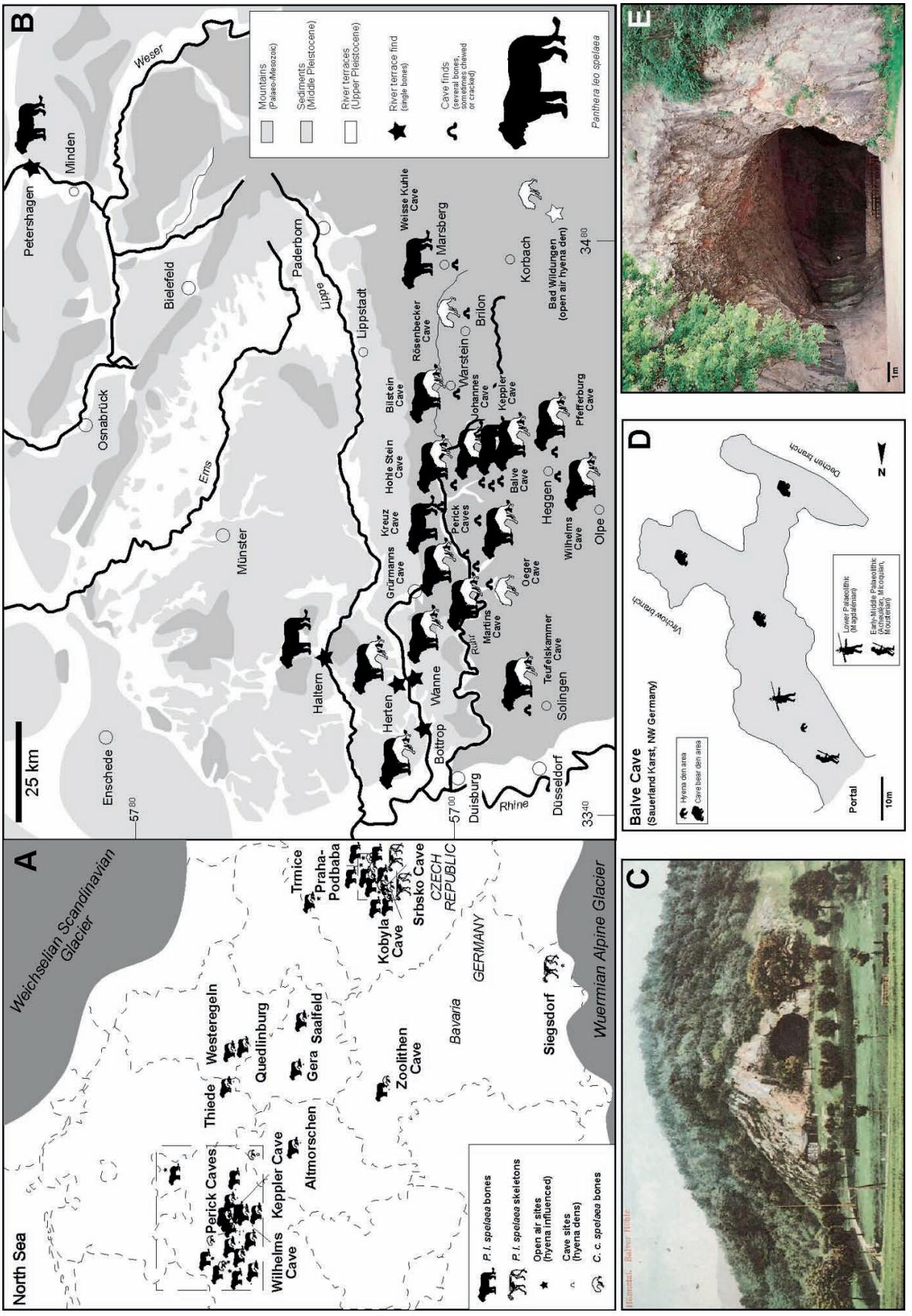


Fig. 1: A. Cave and open air sites with Upper Pleistocene lion material.
The most important are the Bottrop open air site along with the Perick Caves, Wilhelms Cave, Keppler Cave, Bilstein Caves and Balve Cave. Other localities contain only a single or few *Panthera leo spelaea* bone remains. **B. Extension of compared areas all over Germany and Czech Republic. C. Balve Cave portal from historical times (post card). D. Balve Cave map with the Dechen and Virchow branches. E. Modern photo of the Balve Cave entrance portal.**

Fig. 1 : A. Grottes et sites de plein air ayant livré des restes de lion du Pléistocène supérieur. Les plus importants sont le site de plein air de Bottrop et les grottes Perick, Wilhelms, Keppler, Bilstein et Balve. D'autres localités ne contiennent qu'un seul ou quelques restes osseux de Panthera leo spelaea. *B. Extension des zones comparées sur toute l'Allemagne et la République tchèque. C. Entrée de la grotte de Balve à l'époque historique (carte postale). D. Plan de la grotte de Balve avec les branches Dechen et Virchow. E. Photo moderne de l'entrée de la grotte de Balve.*

and Keppler Caves (method after Rabeder *et al*., 2000), whereas Pleistocene radiocarbon data are still missing.

The Balve Cave was mostly historically excavated, and exact stratigraphic documentation, especially of the here-described bone material, is then missing. At least a coarse stratigraphy of a seven meter thick section composed after the descriptions of Virchow (1870), von Dechen (1871), Andrée (1928), Bahnschulte (1940) and Günther (1988) is reproduced here with some new faunal, climatic and cave occupation interpretations (fig. 2). Whereas Bahnschulte (1940) used the Horizon numbers I to V, Günther (1964, 1988) differentiated those former divided I-III layers into the layers 1 to 6 (fig. 2).

The **oldest layer** in the cave is a basal clay which might even be deposited from pre-Pleistocene time. No faunal remains were observed.

The loams of the **first Middle Pleistocene layer** that contain here-determined early forms of cave bears with *Ursus deningeri* (material in the Museum of Humboldt University in Berlin) is of possible late Middle Pleistocene age. The cave was used by early cave bears as a cave bear den cave. At this time, no human impact can be verified. Therefore, this oldest bone layer might even be older than Saalian, and is most likely even of pre-Saalian age. The following four similar layers consisting of non-rounded limestone gravels are dated as Saalian. A Middle Pleistocene age can be estimated, but again, these layers might even be older. At least, they represent a cold period stage. From those layers, cave bears are present, most probably still with *U. deningeri* forms, for which the few materials cannot yet be analysed more in detail. These bone layers also contained *Canis*, and possibly *Praemegaloceros* as well. Even a medium-sized *Panthera pardus* felid can be added to the fauna with a single canine tooth. Perhaps, this cave was at that time also already used by hyenas as a den site, to which imported prey remains of the older layers might be attributed.

The first layer with artefacts is the **Balve I Horizon**, which is separated by layers 5 and 6. The older layer 6 (30-50 cm) is a dark-brown sandy clay containing a few small, and some large, weathered, and rounded limestone pebbles. This layer, which contains late Acheulean artefacts, is of Eemian interglacial age, which is also supported by pollen analyses (Günther, 1988). It was most likely from these layers that *Hippopotamus amphibius* was found (Wollemann, 1887). The younger layer 5 (20-50 cm) is a

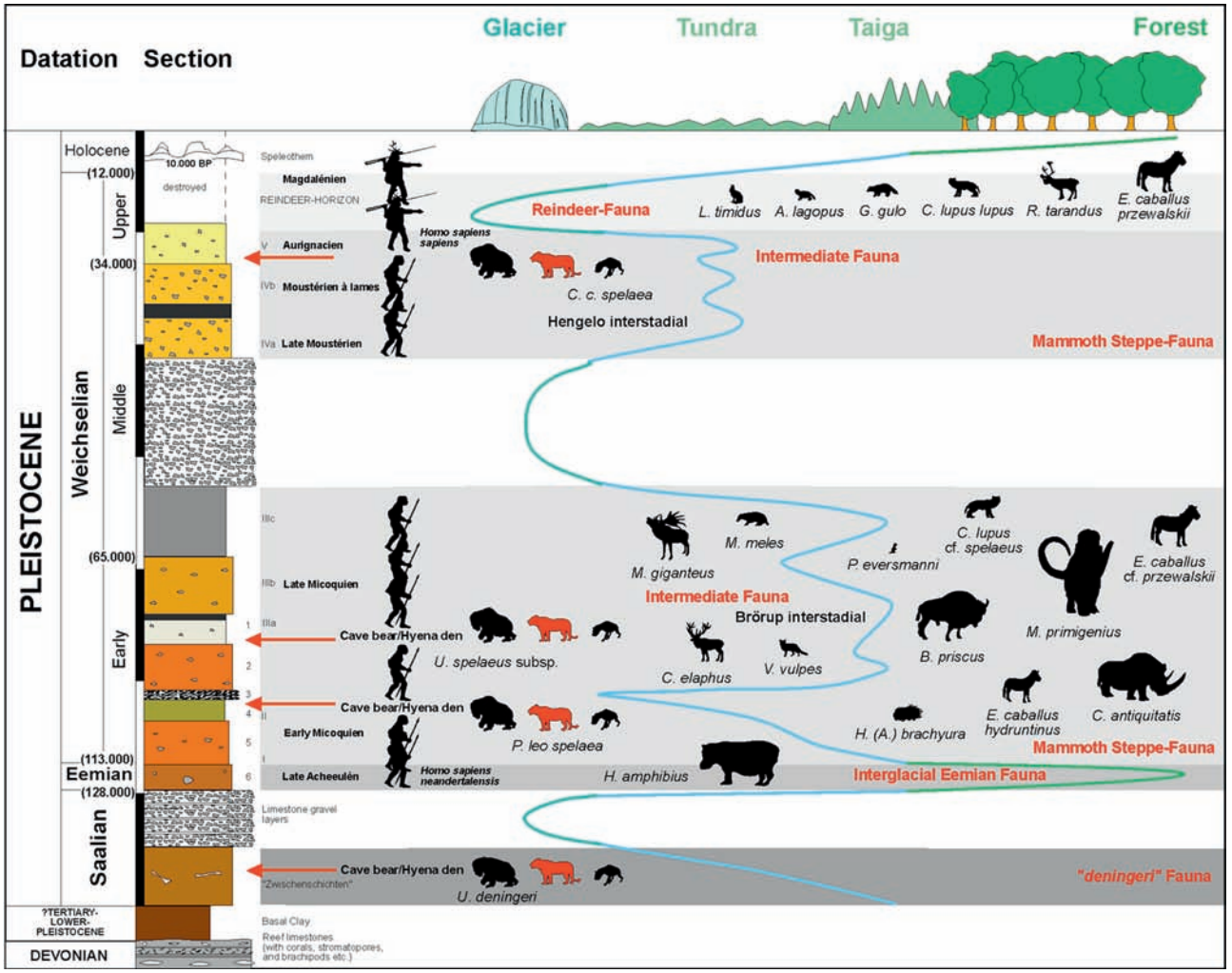


Fig. 2: Generalized stratigraphy of the seven meters thick section of the Balve Cave (NW Germany) and its megafauna content. Stratigraphy reconstructed after Virchow (1870), von Dechen (1871), Andrée (1928), Bahnschulte (1940) and Günther (1988).
Fig. 2 : Coupe stratigraphique de sept mètres d'épaisseur de la grotte de Balve (NO de l'Allemagne) et son contenu en grande faune. Séquence stratigraphique reconstruite d'après Virchow (1870), von Dechen (1871), Andrée (1928), Bahnschulte (1940) et Günther (1988).

red-brown sandy clay with some non-rounded limestone pieces. From these layers, cave bears (*Ursus* cf. *spelaeus* subsp.) and *Coelodonta antiquitatis* are reported (Bahnschulte, 1940). These woolly rhinoceros bones have been redescribed to be mostly of hyena den bone accumulation origin (Diedrich, 2011a). The age of this layer seems to be at the beginning of the early Weichselian.

The **Balve II Horizon** is subdivided into layers 3 and 4. Layer 4 is grey-yellow clay with sharp-edged 1-20 cm large limestones. The rich megafauna indicates a cold climate: *Mammuthus primigenius*, *Bison priscus*, *Equus caballus* cf. *przewalskii*, *Megaloceros giganteus*, *Crocuta crocuta spelaea*, *Ursus* cf. *spelaeus* subsp. and *Canis lupus* cf. *spelaeus.* Several cranial and postcranial bones of the here-described *Panthera leo spelaea* material must originate from those layers. Layer 3 is small grained limestone gravel (6-12 cm in size), which seems to represent the first maximum cold peak of the early Weichselian. Even larger smashed bones from mammoth, which were used as burning material ("bone coal") instead of wood, are present in Horizon I that contains a higher amount of artefacts from the early Micoquian (Günther, 1988).

The **Balve III Horizon** was subdivided into a-c. The oldest, **IIIa Horizon**, is similar to layers 1 and 2. Layer 2 (20-40 cm thick) is made of clay with a few stones. Above it, layer 1 (1-5 cm thick) is represented by light to dark, grey soil, in which small, to coarse, non-rounded limestone pieces are present. Here "bone coal" and artefacts (late Micoquian) are present. Especially from this layer, all three carnivores *Ursus* cf. *spelaeus* subsp., *Crocuta crocuta spelaea* (cf. Diedrich, 2011a) and *Panthera leo spelaea* are reported historically, as well as the typical cold megafauna from the early Weichselian, such as *M. primigenius*, *C. antiquitatis*, *E. caballus* cf. *przewalskii*, *E. hydruntinus*, *M. giganteus* and *R. tarandus*. Even some chew marks from the porcupine *Hystrix* (*A.*) *brachyura* can be included here. They are similar to the rodent gnaw mark shapes recently described for chewed bones from the German open air hyena den site Rote Berg Saalfeld and Czech caves of overlapping European hyena and porcupine dens (Diedrich, 2009c). This layer can be incorporated here to represent hyena activity, den use, and prey importation, because some bones with chew marks and incomplete woolly rhinoceros bones can be referred to this layer (Diedrich, 2011a). The **IIIb Horizon** (30-50 cm thickness) is made of brown-yellow clay with some rounded limestone pebbles, many artefacts (late Micoquian), and animal bones. In the **IIIc Horizon** (80-100 cm) the grey sediments another culture layer is present. This stratum seems to be of middle Weichselian age (Günther, 1988).

A brown-yellow loam with a few stones (60-100 cm thick) was called **Balve-Horizon IV**. It is interrupted in the middle by a 30 cm thick, grey and coal-rich culture horizon. This level is fauna- and artefact-rich. A late Mousterian, and on the top a "Moustérien à lames" lithic inventory has been described, dating into the middle Weichselian (Günther, 1988).

The last preserved **Balve Horizon V** was described as light yellow-grey clay that contained a few small stones. Here, artefacts from the modern human periods of the Aurignacian were figured (Bahnschulte, 1940; Günther, 1988). Therefore, the boundary between the middle and late Weichselian can be set. In these layers, cave bear remains were also excavated, plus a still-mixed mammoth steppe and intermediate fauna. From this Aurignacian period, a horse head engraving was published as the only art find (Andrée, 1933).

Younger modern human archaeological layers of a Magdalenian period were destroyed in the past and sediments or sections are missing from the "Reindeer horizon" (cf. Günther, 1988). As compared to historical descriptions and still present bone material, the typical megafauna featuring the three large carnivores *Panthera*, *Ursus* and *Crocuta* is absent. In those final Weichselian layers, there is an abundance of reindeer *Rangifer tarandus* remains, including many dropped antlers that have no carnivore bite or chew marks. Those must have been collected and accumulated by humans and not by hyenas or other carnivores (wolves). Additionally *Equus caballus* cf. *przewalskii*, horses (see classification in Zessin *et al*., 2009) and wolves are present, as is finally the only musk ox *Ovibos moschatus* remain (Andrée, 1933), which fits to the maximum cold period, and periods after this, of the late Weichselian. Artefacts seem to be all of the final Magdalenian time of the V and VI stages (Günther, 1988).

The late Palaeolithic horizon was covered by a thick speleothem layer, which was dated between 8,000-10,000 yr BP (Zygowski, 1988), but for which a new modern dating is still lacking.

Above this layer Neolithic and early pre-Roman Iron Age (La Tène) artefacts and ceramics were identified from the Balve Cave youngest archaeological layers (Brandt, 1939; Bleicher, 1983, 1991).

3 - MATERIAL AND METHODS

The studied lion bone material of the Balve and other Sauerland caves are from the collections of the Museum Burg Altena (MBA). The unlabelled and not even well-cleaned material was rediscovered within these studies. Only one hyena maxillary and about 60 teeth, less postcranial bones (mainly from the cave bear), and also several mammoth teeth, represent this Balve Cave material, which also includes about hundred palaeolithic artefacts. Other material from C. Kremer (old labels on the bones with his name) was studied in the Goldfuss-Museum Bonn (GMB); not lion remains, but hyena and "nibbling stick" remains. The most important historical hyena and prey bone collection is from the Museum Balve (MB), which is partly on displayed and with other remains including lion material stored in the Archaeological Museum Herne. In the Emschertalmuseum Schloß Strünckede Herne (EMSH), a few bones, including hyena and lion, are deposited. A large part of the Balve Cave (coll. Kremer 1873), Martins Cave (coll. Schaaffhausen 1875; Schmitz 1889), or Wilhelms Cave (coll. Hundt and Troschel 1874) bone collections are mainly in the Geol-

ogisch-Paläontologische Museum of the Westphalian Wilhelms-University Münster (GPIM) but also in the GMB. Bones from the Keppler Cave, Hohle Stein Cave, or Johannes Cave, are housed in the Stadtmuseum Menden (SMM). Finally, a few non-lion bones (e.g. hyena) are in the collection of the Museum für Natur und Umwelt Osnabrück (MNUO). A lion jaw from the Kreuz Cave is in the Dechenhöhlenmuseum Lethmathe (DHM).

The work was made to understand the lion bone presence at hyena den type sites from the palaeobiological point of view in the Sauerland Karst region at thirteen hyena cub raising, commuting, and prey accumulation sites (fig. 3).

None of the Balve Cave lion bones have exact stratigraphic context or labels with further information, but bones from older Middle Pleistocene layers are preserved different as from younger layers, and are more fossilized. The Middle Pleistocene bones generally have typical black manganese dendritic surfaces, and break due to beginning lithifications. The colour is more reddish and irregular. Late Pleistocene bones are not fossilized, have no dendritic surfaces and are more yellow to brownish in colour. Even with those helpful criteria it is too vague to present a list with their Saalien or Weichselian ages. In some cases the material might be distinguished from each other, but not in all cases, which makes again difficult a statistical analyses and identification for each bone. After the preservation degree, about 85 % and even more of the bones of Balve Cave might be expected to be from the late Pleistocene (early to middle Weichselian), and only a few seem to be from the late Middle Pleistocene (late Saalian). This generally is coincident to the amount of all bone material (mostly from early to late Weichselian), which is barely represented in the oldest layers. The Saalian horizons were historically not much excavated,

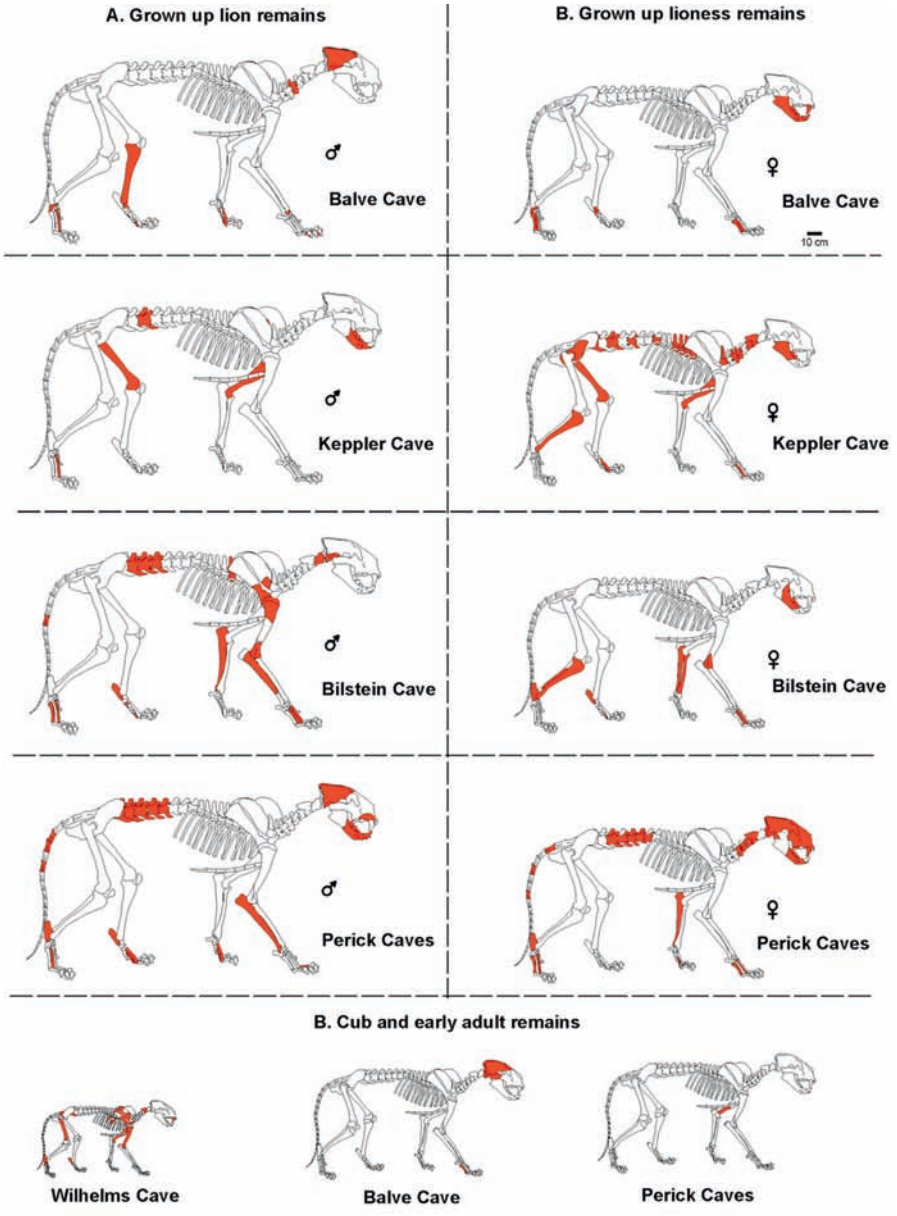


Fig. 3: *Panthera leo spelaea* (Goldfuss 1810) skeleton part remains from the Balve Cave and other caves of the Sauerland Karst Mountains (NW Germany), all being from cave bear or hyena dens.
Fig. 3 : Représentation anatomique des restes de Panthera leo spelaea *(Goldfuss 1810) de la grotte de Balve et d'autres grottes des montagnes karstiques du Sauerland (NO de l'Allemagne), toutes étant des repaires d'ours des cavernes ou des tanières de hyène.*

because they often did not reach deep or even the cave base. The stratigraphic information about the finds is therefore limited. As demonstrated in the stratigraphy, there are three late Pleistocene horizons which must have produced the here-described lion material, whereas in the historical description, *Panthera* bones are only mentioned for the early Weichselian layers.

With the historical lion bone material from the Sauerland Karst at least sex identification was tried for complete bones, whereas an individual age statistics is the most valuable information, such as taphonomic studies including bone damages and bite marks caused by carnivores. Also the bone frequency to estimate the body part presence is presented, but the material from all caves again is too few for a good data base (fig. 3).

Family Felidae Gray 1821
Genus *Panthera* Oken 1816
Panthera leo spelaea (Goldfuss 1810)
(fig. 4, 5, 6, 7, 8, 9 and 10)

3.1 - BALVE CAVE MATERIAL

Two brain cases of incomplete skulls, a few incomplete mandibles, some isolated teeth, one complete tibia, astragals and calcanei, but mainly metapodials and phalangae; in total 56 bones (tab. 1). Most of the material is not strongly fossilized and most probably mainly from the early to middle Upper Pleistocene layers. Only main measurements are given for possible comparative sex identifications.

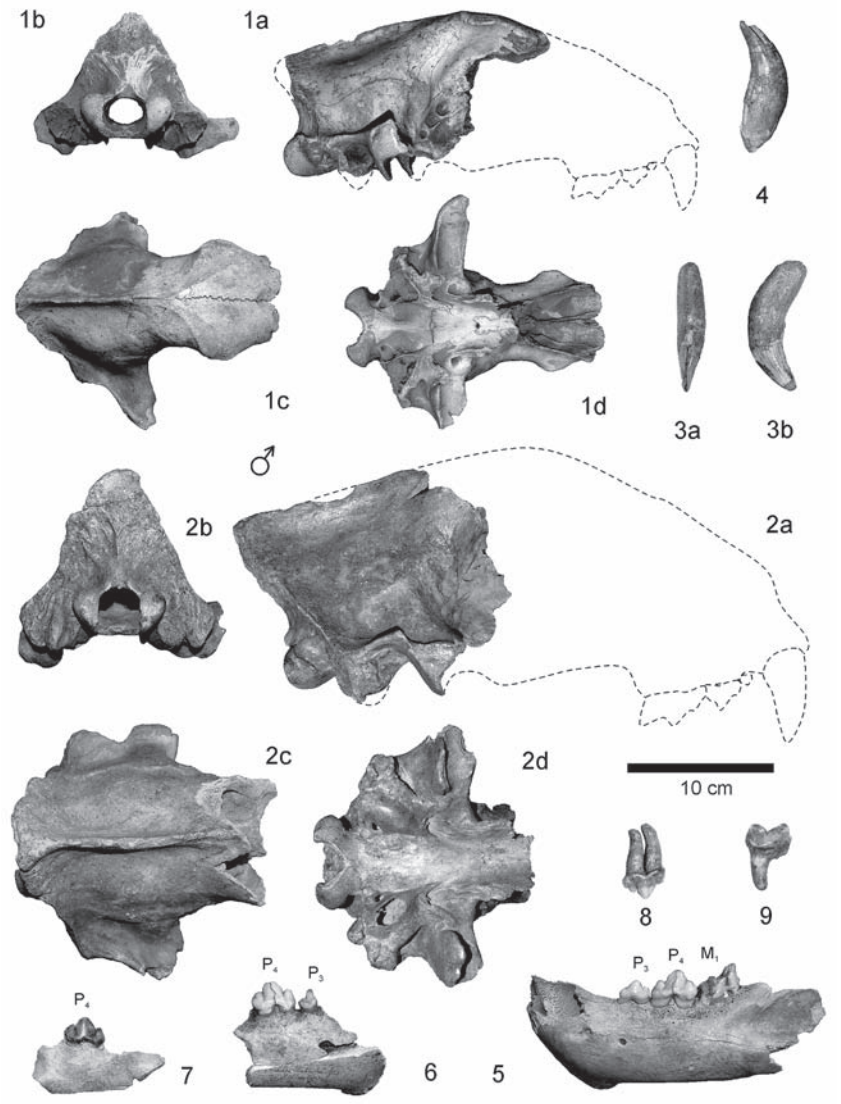


Fig. 4: ***Panthera leo spelaea*** **(Goldfuss 1810) cranial remains from the Balve Cave (NW Germany).** 1. Brain case from a young adult lioness (MB No. Balve-1): a. lateral right, b. occipital, c. dorsal, d. ventral. 2. Brain case from an old adult to senile lion (MB No. Balve-2): a. lateral right view, b. occipital view, c. dorsal view, d. ventral view. 3. Left upper jaw canine from an adult individual (GPIM No. A5F1297): a. caudal view, b. labial view. 4. Right lower jaw canine from an adult animal (MB No. Balve-4): labial view. 5. Left mandible from a lioness (MB No. 861): lateral left view. 6. Mandible fragment from a lioness (MB No. Balve-3): lateral right view. 7. Left mandible fragment (EMSH No. Bal-1): lateral view. 8. Right upper jaw P^3 from an adult animal (GPIM No. A5F1265): labial view. 9. Left lower jaw M_1 from a senile animal (GPIM No. A5F1296): labial view.
Fig. 4 : Restes crâniens de Panthera leo spelaea *(Goldfuss 1810) de la grotte de Balve (NO de l'Allemagne). 1. Crâne d'une jeune lionne adulte (MB No. Balve-1) : a. vue latérale droite, b. vue occipitale, c. vue dorsale, d. vue ventrale. 2. Crâne d'un lion âgé à sénile (MB No. Balve-2) : a. vue latérale droite, b. vue occipitale, c. vue dorsale, d. vue ventrale. 3. Canine gauche d'un individu adulte (GPIM No. A5F1297) : a. vue caudale, b. vue labiale. 4. Canine inférieure droite d'un animal adulte (MB No. Balve-4) : vue labiale. 5. Mandibule gauche d'une lionne (MB No. 861) : vue latérale gauche. 6. Fragment de mandibule d'une lionne (MB No. Balve-3) : vue latérale droit. 7. Fragment de mandibule gauche (EMSH No. Bal-1) : vue latérale. 8. P^3 droite supérieure d'un animal adulte (GPIM No. A5F1265) : vue latérale. 9. M_1 gauche inférieure d'un animal sénile (GPIM No. A5F1296) : vue latérale.*

No.	Coll.-No..	Bone-type	Commentary	Left	Rigth	Sex	Age	Colletion
1	Balve-1	Skull	Brain case, total length 192 mm, frontal width 81 mm. Occipital to frontal length 155 mm, occipital width 61 mm, all brain case bones unfused			Female	Young adult	Museum Balve
2	Balve-2	Skull	Brain case, total length 170 mm, occipital width 69 mm			Male	Older adult to senile	Museum Balve
3	861	Lower jaw	Without ramus and all I, P_4 length 29 mm, M_1 with old broken tips	x		Female	Senile	Museum Balve
4	Balve-3	Lower jaw	Symphyse fragment, with P_{3-4}, P_4 length 29 mm		x	Female	Adult	Museum Balve
4	Bal-1	Lower jaw	Fragment with P_4	x			Adult	Emschertalmuseum Schloß Strünckede Herne
5	A5F1297	Tooth	Upper jaw canine	x		Female	Adult	Geologisch-Paläontologisches Museum, WWU Münster
6	Balve-4	Tooth	Lower jaw canine		x	Female	Adult	Museum Balve
7	Balve-5	Tooth	Lower jaw canine fragment					Museum Balve
8	Balve-6	Tooth	Lower jaw canine fragment					Museum Balve
9	A5F1265	Tooth	Upper jaw P_3, length 30 mm		x	Male	Adult	Geologisch-Paläontologisches Museum, WWU Münster
10	A5F1296	Tooth	Lower jaw M_1, length 32 mm	x		Male	Senile	Geologisch-Paläontologisches Museum, WWU Münster
11	A51022	Scapholunatum	Complete		x		Adult to senile	Geologisch-Paläontologisches Museum, WWU Münster
12	A51023	Capitatum	Complete		x		Adult to senile	Geologisch-Paläontologisches Museum, WWU Münster
13	Balve-12	Metacarpus	Mc II, length 112 mm	x		Male	Adult to senile	Museum Balve
14	Balve-13	Metacarpus	Mc IV, half	x			Adult to senile	Museum Balve
15	Balve-8	Metacarpus	Mc IV, length 131 mm belongs to Balve 7		x	Female	Adult to senile	Museum Balve
14	Balve-7	Metacarpus	Mc V, length 111 mm belongs to Balve 8		x	Female	Adult to senile	Museum Balve
15	Balve-9	Metacarpus	Mc V, length 109 mm, distal incomplete belongs to Balve 8		x	Female	Older juvenile	Museum Balve
16	Balve-10	Metacarpus	Mc V, length 105 mm		x		Young adult	Museum Balve
17	Balve-11	Metacarpus	Mc V, length 115 mm	x		Male	Adult to senile	Museum Balve
18	Balve-41	Phalanx I	Digit II of the manus		x		Adult to senile	Geologisch-Paläontologisches Museum, WWU Münster
19	A5F1182	Phalanx I	Digit III of the manus		x		Adult to senile	Museum Balve
20	Balve-37	Phalanx I	Digit IV of the manus		x		Adult to senile	Museum Balve
21	A5F1183	Phalanx I	Digit IV of the manus	x			Adult to senile	Geologisch-Paläontologisches Museum, WWU Münster
22	Balve-40	Phalanx I	Digit IV of the manus	x			Adult to senile	Geologisch-Paläontologisches Museum, WWU Münster
23	A5F1184	Phalanx I	Digit V of the manus	x			Adult to senile	Museum Balve
24	A51024	Cervical vertebra	C5, incomplete				Adult to senile	Geologisch-Paläontologisches Museum, WWU Münster
25	Balve-14	Tibia	Complete, length 381 mm, distal width 67 mm	x		Male	Adult to senile	Museum Balve
26	Balve-15	Astragal	Incomplete, length 71 mm, width 75 mm	x		Male	Adult to senile	Museum Balve
27	Balve-16	Astragal	Incomplete, length 65 mm		x	Female	Adult to senile	Museum Balve
28	Balve-17	Astragal	Fragment		x		Adult to senile	Museum Balve
29	Balve-18	Astragal	Incomplete, length 62 mm, width	x		Female	Adult to senile	Museum Balve
30	Balve-19	Astragal	Incomplete, length 68 mm, width 61 mm		x		Adult to senile	Museum Balve
31	Balve-20	Astragal	Incomplete, length 65 mm, width	x		Female	Adult to senile	Museum Balve
32	A51025	Cuboid	Complete	x			Adult to senile	Geologisch-Paläontologisches Museum, WWU Münster
33	A51026	Sesamoid	Complete				Adult to senile	Geologisch-Paläontologisches Museum, WWU Münster
34	A51027	Sesamoid	Complete				Adult to senile	Geologisch-Paläontologisches Museum, WWU Münster
35	Balve-32	Metatarsus	Mt II, without distal joint		x	Female	Adult to senile	Museum Balve
36	Balve-29	Metatarsus	Mt III, Length 153 mm		x	Male	Adult to senile	Museum Balve
37	Balve-31	Metatarsus	Mt III, Length 153 mm		x	Male	Adult to senile	Museum Balve
38	Balve-30	Metatarsus	Mt IV, Length 141 mm		x	Female	Adult to senile	Museum Balve
39	Balve-43	Metatarsus	Mt IV, 142 mm		x	Female	Adult to senile	Museum Balve
40	Balve-28	Metatarsus	Mt IV, Length 154 mm	x		Male	Adult to senile	Museum Balve
41	Balve-22	Metatarsus	Mt IV, Belongs to Balve-21		x	Female	Adult to senile	Museum Balve

Tab. 1: *Panthera leo spelaea* (Goldfuss 1810) bone remains from the Balve Cave (NW Germany).
Tab. 1 : Restes osseux de Panthera leo spelaea *(Goldfuss 1810) de la grotte de Balve (NO de l'Allemagne).*

Fig. 5: ***Panthera leo spelaea*** **(Goldfuss 1810) vertebra, fore and hind limb bone remains from the Balve Cave (NW Germany).** 1. Cervical vertebra No. 5 (GPIM No. A51022): a. dorsal view, b. cranial view. 2. Right mc IV and V from a lioness (MB No. Balve-7/8): dorsal view. 3. Right mc V of a young adult animal (MB No. Balve-10): dorsal view. 4. Left mc V from an adult lion (MB No. Balve-11): dorsal view. 5. Left mc II from an adult lion (MB No. Balve-12): dorsal view. 6. Right scapholunatum (GPIM No. A51023): dorsal view. 7. Right capitatum (GPIM No. A51024): cranial view. 8. Left tibia from an adult lion (MB No. Balve-14): cranial view. 9. Left astragal from an adult lion (MB No. Balve-15): dorsal view. 10. Left astragal from an adult lioness (MB No. Balve-18): dorsal view. 11. Left cuboid (GPIM No. A51025): cranial view. 12. Left mt V of an adult lion (MB No. Balve-23): dorsal view. 13. Left mt V from an adult lion (MB No. Balve-24): dorsal view. 14. Right mt IV and V from an adult lioness (MB No. Balve-21/22): dorsal view. 15. Right mt IV from an adult lioness (MB No. Balve-30): dorsal view. 16. Right mt IV from an adult lioness (MB No. Balve-43): dorsal view. 17. Left mt IV of an adult lion (MB No. Balve-28): dorsal view. 18. Right mt III from an adult lion (MB No. Balve-29): dorsal view. 19. Right mt III from an adult lion (MB No. Balve-31): dorsal view. 20. Half phalanx I digit I (MB No. Balve-36): dorsal view. 21. Sesamoid (GPIM No. A51026): lateral view. 22. Sesamoid (GPIM No. A51027): lateral view. 23. Phalanx I right digit IV from the manus (MB No. Balve-37): dorsal view. 24. Phalanx I left digit IV from the pes (MB No. Balve-38): dorsal view. 25. Phalanx I left digit III from the pes (MB No. Balve-39): dorsal view. 26. Phalanx I left digit IV from the manus (MB No. Balve-40): dorsal view. 27. Phalanx I right digit III from the manus (GPIM No. A5F1182): dorsal view. 28. Phalanx I left digit V from the manus (GPIM No. A5F1184): dorsal view. 29. Phalanx I right digit II from the manus (MB No. Balve-41): dorsal view. 30. Phalanx I left digit IV from the manus (GPIM No. A5F1183): dorsal view. 31. Phalanx I left digit V from the pes (MB No. Balve-42): dorsal view. 32. Phalanx II (GPIM No. A51028): dorsal view. 33. Phalanx II (GPIM No. A51029): dorsal view.

Fig. 5 : Vertèbres et os des membres antérieurs et postérieurs de Panthera leo spelaea *(Goldfuss 1810) de la grotte de Balve (NO de l'Allemagne). 1. Vertèbre cervicale n° 5 (GPIM No. A51022) : a. vue dorsale, b. vue crâniale. 2. Métacarpien IV et V droits d'une lionne (MB No. Balve-8/7) : vue dorsale. 3. Métacarpien V droit d'un animal adulte jeune (MB No. Balve-10) : vue dorsale. 4. Métacarpien V gauche d'un lion adulte (MB No. Balve-11) : vue dorsale. 5. Métacarpien II gauche d'un lion adulte (MB No. Balve-12) : vue dorsale. 6. Scapho-lunatum droit (GPIM No. A51023) : vue dorsale. 7. Capitatum droit (GPIM No. A51024) : vue crâniale. 8. Tibia gauche d'un lion adulte (MB No. Balve-14) : vue crâniale. 9. Astragale gauche d'un lion adulte (MB No. Balve-15) : vue dorsale. 10. Astragale gauche d'une lionne adulte (MB No. Balve-18) : vue dorsale. 11. Cuboïde gauche (GPIM No. A51025) : vue crâniale. 12. Métatarsien V gauche d'un lion adulte (MB No. Balve-23) : vue dorsale. 13. Métatarsien V gauche d'un lion adulte (MB No. Balve-24) : vue dorsale. 14. Métatarsien IV et V droits d'une lionne adulte (MB No. Balve-21/22) : vue dorsale. 15. Métatarsien IV droit d'une lionne adulte (MB No. Balve-30) : vue dorsale. 16. Métatarsien IV droit d'une lionne adulte (MB No. Balve-43) : vue dorsale. 17. Métatarsien IV gauche d'un lion adulte (MB No. Balve-28) : vue dorsale. 18. Métatarsien III droit d'un lion adulte (MB No. Balve-29) : vue dorsale. 19. Métatarsien III droit d'un lion adulte (MB No. Balve-31) : vue dorsale. 20. Phalange I (MB No. Balve-36) : vue dorsale. 21. Sésamoïde (GPIM No. A51026) : vue latérale. 22. Sésamoïde (GPIM No. A51027) : vue latérale. 23. Phalange I du doigt IV de la main droite (MB No. Balve-37) : vue dorsale. 24. Phalange I du doigt IV du pied gauche (MB No. Balve-38) : vue dorsale. 25. Phalange I du doigt III du pied gauche (MB No. Balve-39) : dorsale. 26. Phalange I du doigt IV de la main gauche (MB No. Balve-40) : dorsale. 27. Phalange I doigt III de la main droite (GPIM No. A5F1182) : dorsale. 28. Phalange I du doigt V de la main gauche (GPIM No. A5F1184) : dorsale. 29. Phalange I du doigt II de la main droite (MB No. Balve-41) : vue dorsale. 30. Phalange I du doigt IV de la main gauche (GPIM No. A5F1183) : vue dorsale. 31. Phalange I du doigt V du pied gauche (MB No. Balve-42) : vue dorsale. 32. Phalange II (GPIM No. A51028) : vue dorsale. 33. Phalange II (GPIM No. A51029) : vue dorsale.*

The **first skull** is, in its preservation, typical of late Pleistocene bone material. This one is small in proportions and consists only of the brain case (fig. 4.1). The cranial bones are not well-fused. The sagittal crest is already developed indicating an age of an older juvenile to a young adult animal. The measurements of the condyle width (61 mm) and frontals width (81 mm) would match young female skulls too. A total length of the brain case of 192 mm can be given with an estimated short total length of about 300 mm. The posterior brain case damage is similar to the damage on the second skull; this is old damage that seems to be the result of carnivore

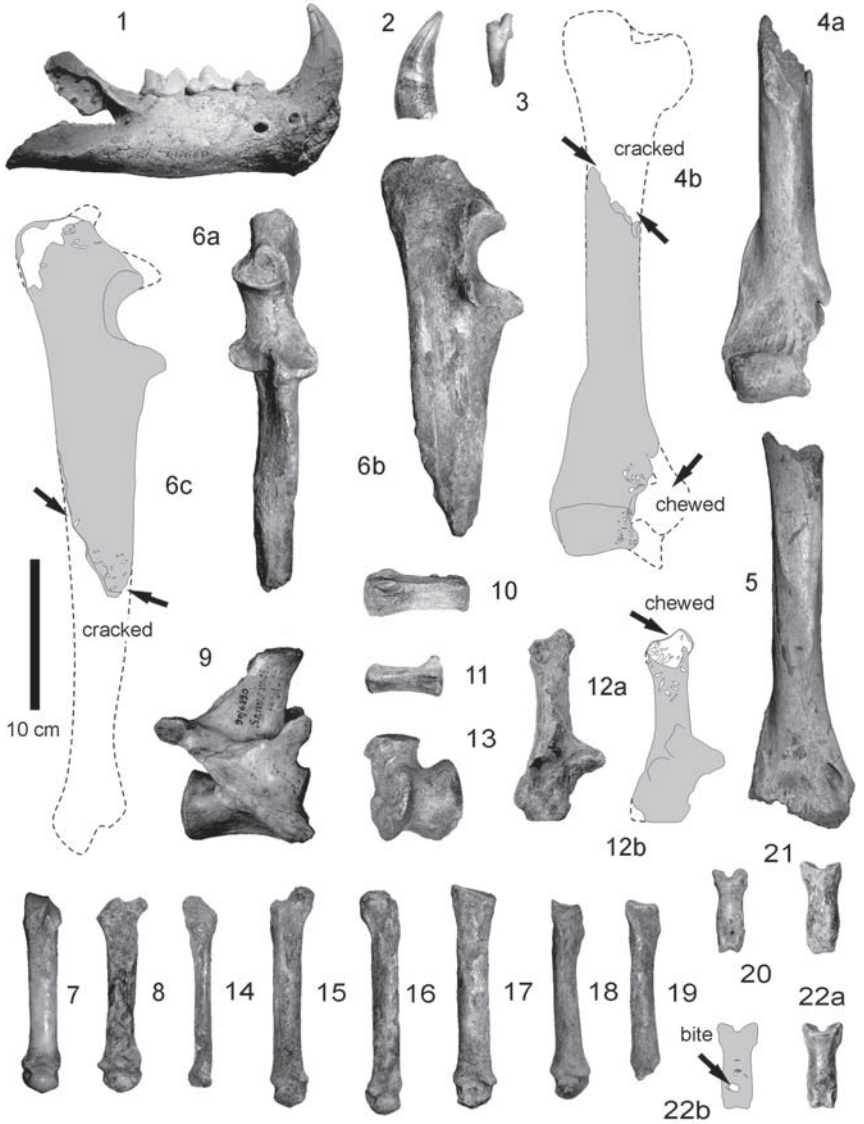


Fig. 6: ***Panthera leo spelaea*** **(Goldfuss 1810) remains from different Sauerland Karst Mountain caves (NW Germany).** 1. Right mandible from the Kreuz Cave (DHM No. Kreuz-1): lateral view. 2. Lower jaw canine from the Grürmanns Cave (GPIM No. A5F1275): lateral view. 3. P tooth fragment from the Martins Cave (GPIM No. A5F1276): lateral view. 4. Left cracked humerus of a lioness from the Teufelskammer Cave (GMB No. M5832): cranial view. 5. Left humerus shaft from the Hohle Stein Cave (SMM No. 90/5523): cranial view. 6. Right cracked ulna from the Martins Cave (GPIM No. A5F1231a): a-b. lateral view, c. cranial view. 7. Right mc IV from the Johannes Cave (SMM No. 90/6528): dorsal view. 8. Left mc II from the Martins Cave (GMB No. M2466): dorsal view. 9. Lumbar vertebra no. 6 from the Johannes Cave (SMM No. 90/6390): lateral view. 10. Upper caudal vertebra from the Grürmanns Cave (GPIM No. A5F1274): lateral view. 11. Middle caudal vertebra from the Martins Cave (GPIM No. A5F1196): lateral view. 12. Right calcaneus (GPIM No. A5F1231): cranial view. 13. Right astragalus from the Martins cave (GMB No. M2460): dorsal view. 14. Right mt V from the Martins cave (GPIM No. A5F1231): cranial view. 15. Left mt IV from the Martins cave (GBM No. M2462): dorsal view. 16. Right mt IV from the Martins cave (GBM No. M2470a): dorsal view. 17. Right mt III from the Martins Cave (GMB No. M2470): dorsal view. 18. Right mt II from the Martins cave (GMB No. M2463): dorsal view. 19. Rigth mt II from the Martins cave (GMB No. M2464): dorsal view. 20. Phalanx I from the Martins Cave (GPIM No. A5F1185): dorsal view. 21. Phalanx I from the Martins Cave (GPIM No. A5F1197): dorsal view. 22. Phalanx I from the Martins Cave (GPIM No. A5F1198): dorsal view.

Fig. 6 : Restes de Panthera leo spelaea *(Goldfuss 1810) provenant de différentes grottes des montagnes karstiques du Sauerland (NO de l'Allemagne). 1. Mandibule droite de la grotte Kreuz (DHM No. Kreuz-1): vue latérale. 2. Canine inférieure de la grotte Grürmanns (GPIM No. A5F1275): vue latérale. 3. Fragment de prémolaire de la grotte Martins (GPIM No. A5F1276): vue latérale. 4. Humérus gauche fracturé d'une lionne de la grotte Teufelskammer (GMB No. M5832): vue crâniale. 5. Humérus gauche de la grotte de Hohle Stein (SMM No. 90/5523): vue crâniale. 6. Ulna droite fracturé de la grotte Martins (GPIM No. A5F1231a): a-b. vue latérale, c. vue crâniale. 7. Métacarpien IV droit de la grotte Johannes (SMM No. 90/6528): vue crâniale. 8. Métacarpien II gauche de la grotte Martins (GMB No. M2466): vue crâniale. 9. Sixième vertèbre lombaire de la grotte Johannes (SMM No. 90/6390): vue latérale. 10. Vertèbre caudale proximale de la grotte Grürmanns (GPIM No. A5F1274): vue latérale. 11. Vertèbre caudale intermédiaire de la grotte Martins (GPIM No. A5F1196): vue latérale. 12. Calcanéum droit (GPIM No. A5F1231): vue crâniale. 13. Astragale droit de la grotte Martins (GMB No. M2460): vue dorsale. 14. Métatarsien V droit de la grotte Martins (GPIM No. A5F1231): vue crâniale. 15. Métatarsien IV gauche de la grotte Martins (GBM No. M2462): vue crâniale. 16. Métatarsien IV droit de la grotte Martins (GBM No. M2470): vue crâniale. 17. Métatarsien III droit de la grotte Martins (GMB No. M2470): vue crâniale. 18. Métatarsien II droit de la grotte Martins (GMB No. M2463): vue crâniale. 19. Métatarsien II droit de la grotte Martins (GMB No. M2464): vue crâniale. 20. Phalange I de la grotte Martins (GPIM No. A5F1185): vue dorsale. 21. Phalange I de la grotte Martins (GPIM No. A5F1197): vue dorsale. 22. Phalange I de la grotte Martins (GPIM No. A5F1198): vue dorsale.*

activities, such as hyenas scavenging damage. The dentition is absent.

The **second skull** (fig. 4.2) is much larger in its brain case proportions compared to the first skull. Again, the saggital area is missing parts. The anterior brain case has modern fractures; originally the skull possibly had its maxillaries. The occipital width (69 mm) is large and fits to grown up and male skulls as discussed later. The total preserved length is 170 mm. As a result of its completely fused brain case sutures, the individual was an older adult.

A single **maxillary** canine from an adult individual is present (fig. 4.3). The root is completely closed and the sharp edges are not rubbed, supporting an adult individual age. Only one lower jaw canine, which is slightly incomplete in its enamel area (fig. 4.4), is from an adult animal with small proportions.

The lower jaws are all incomplete. The most complete left one (fig. 4.5) lacks the ramus due to modern damage, but has the P_{3-4} and M_1 teeth. The width of the molar cannot be measured, as it was proximally broken during the lifetime of this old adult animal, and slightly polished. The P_4 length is 29 mm. A second right mandible (fig. 4.6) is represented by its anterior part with half of the P_3 and the P_4. The small P_4 length is 29 mm. The third mandible is a fragment including the P_4 (fig. 4.7). Only two teeth, a complete right upper P^3 (length 30 mm) from an adult animal (fig. 4.8), and a left lower M_1 without parts of the root (fig. 4.9), from a senile one, are preserved in the material.

The **fore limbs** are missing all long bones. This is most likely a problem of historical collecting, material selection and loss. At least seven metacarpi and six first phalangae are preserved. The gender of the metacarpi can be possibly determined by its proportions; however it is impossible to make this determination for the phalangae. The metarcarpi (fig. 5.2, 5.3, 5.4 and 5.5), all from adult individuals, are listed in table 1 with main data and most probable sex identifications.

Important are the two metacarpi that fit (fig. 5.2) because of their similar preservations and small proportions. This indicates the presence of originally articulated pedal skeletons at the cave site. Strong different proportions are not only visible in the two mc V (fig. 5.3 and 5.4). The phalangae (fig. 5.23-33), are from different digit positions of the manus (see also tab. 1).

The **hind limbs** are represented at least by one long bone, a left tibia (fig. 5.8), from an adult male lion. Thirteen metatarsi, all from adult animals are the dominant bone types – all data are in table 1. To mention are the different proportions (cf. fig. 5) and two well-matching right metatarsi IV/V (fig. 5.14). The latter ones prove articulated pedal skeletons at the cave site. The phalangae I are well-represented in the material; their digit position can mostly be given. Manus and pes phalanges are from different positions as mentioned (see tab. 1, fig. 5.23 to 33).

3.2 - BILSTEIN CAVE MATERIAL

The Upper Pleistocene Bilstein Cave lion material from this cave bear den (show cave) with short hyena occupation in the entrance area was monographically figured and described (Diedrich, 2009d). 39 bones are present from all body parts of different male and female individuals; all adult are old in age. Only one bone is from a young adult animal.

3.3 - GRÜRMANNS CAVE MATERIAL

A single modern broken canine of an adult animal is the first remain from this hyena den cave (fig. 7.2); the second is an upper caudal vertebra (fig. 7.10).

3.4 - HOHLE STEIN CAVE MATERIAL

From this destroyed small hyena prey depot cave at the beginning of the Hönnetal, a single small-sized and modern damaged shaft, probably from an early adult animal (fig. 6.5), is the only lion remain.

3.5 - JOHANNES CAVE MATERIAL

Also this small cave destroyed around 1944 was a hyena den. Lion remains are a metapod (fig. 6.7), and a lumbar vertebra (fig. 6.9), both remains from grown up individuals.

3.6 - KEPPLER CAVE MATERIAL

The Keppler Cave in the Hönnetal was opposite to the Balve Cave and is completely destroyed today. In total, 33 bones are preserved in the large cave bear dominated bone collection (fig. 7, 8 and 9, tab 2), which show, in some cases, modern fractures as a result of the historical excavations. Three mandibles and two isolated lower jaw teeth (M_1) are the cranial remains. The first right lower jaw (fig. 7.1) has modern fractures all over. The P_{3-4} and M_1 teeth are slightly rubbed, indicating an adult animal age. The width of the M_1 (29 mm) is quite small. The second left mandible (fig. 7.2) has no ramus and only the P_{3-4} and M_1 teeth. The latter posterior tip was broken during the animal life, indicating an older adult age by its tooth wear. The small proportions, such as the mandible height between the P_4/M_1 (47 mm) are slender; also the M_1 is only 24 mm in length. The third left mandible (fig. 7.3) is strongly encrusted by a speleothem layer. Only the P_4/M_1 are preserved; the molar has old fractured tips indicating an older adult individual. The two isolated teeth from adults are both M_1 (right and left) and each is 27 mm in length.

The fore limb bones are three right humeri (fig. 7.6, 7.7 and 7.8); two of them are very long (360 and 362 mm), only one is much shorter (342 mm length). All are adult to older individual remains. The lioness humerus has 2-3 mm thin bite scratch marks on the shaft (fig. 7.7b). Two left metacarpi IV (fig. 7.9 and 7.10) are again from adult to old animals; they are short in their lengths (117/122 mm).

A large amount of 16 vertebrae consists of four cervical, eight thoracic and four lumbar vertebra, all generally missing parts of the processi because of modern fractures. The second cervical vertebra, the axes (fig. 8.1), the third (fig. 8.2), the fifth (fig. 8.3) and the sixth (fig. 8.4) are all quite small in size. They might even belong to one skeleton. Also, the thoracic vertebrae seem to not be represented twice. The T1 (fig. 8.5) is quite small and, whereas the T2 (fig. 8.6) is large. There are four more middle to posterior thoracic small-proportioned vertebrae; a T4 (fig. 8.7), T7 (fig. 8.8), T8 (fig. 8.9), T9 (fig. 8.10), T10 (fig. 8.11), and finally a complete T14 (fig. 8.12). Four lumbar vertebra consist of one L3 (fig. 8.13), whereas one L5 is also smaller (fig. 8.14). The other similar L5 is larger (fig. 8.15). Finally a sixth lumbar vertebra (fig. 8.16) is again smaller sized.

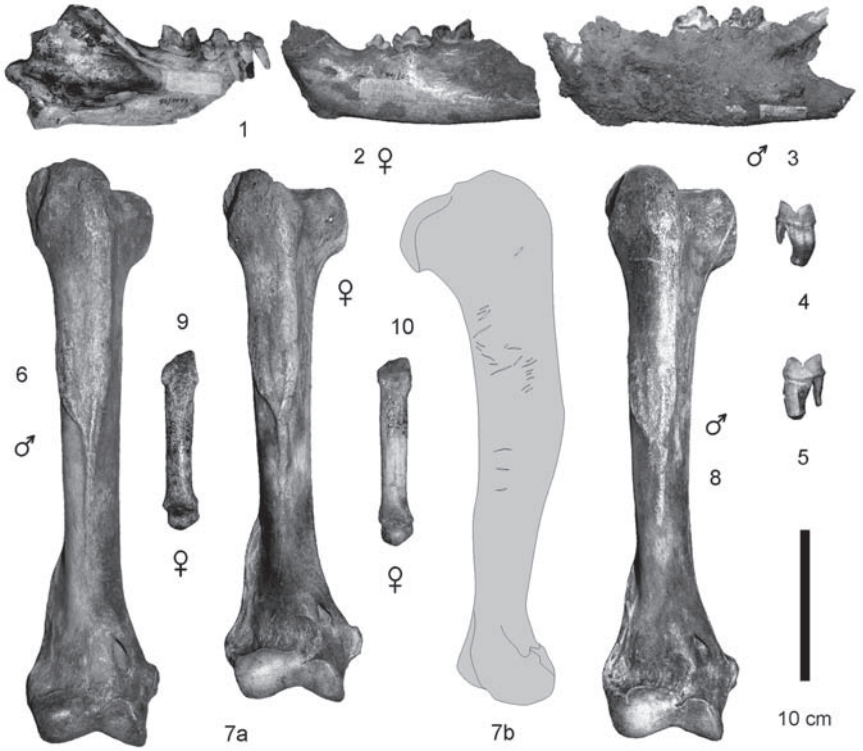


Fig. 7: *Panthera leo spelaea* (Goldfuss 1810) cranial and fore limb remains from Keppler Cave of the Sauerland Karst Mountains (NW Germany). 1. Right mandible of an adult lioness (SKMM No. 90/7047): lateral view. 2. Left mandible of an adult female (SKMM No. 90/7046): lateral view. 3. Left mandible of an adult male (SKMM No. 90/6495): lateral view. 4. Right M_1 of an adult lioness (SKMM No. 90/7048a): labial view. 5. Left M_1 of an adult lioness (SKMM No. 90/7048b): labial view. 6. Right humerus of an adult to senile male (SKMM No. 90/6521): cranial view. 7. Right humerus of an adult to senile lioness (SKMM No. 90/6520): a. cranial view, b. lateral view, right with bite scratches. 8. Right humerus of an adult to senile male (SKMM No. 90/6522): cranial view. 9. Left Mc IV of an adult to senile lioness (SKMM no. 90/6531): cranial view. 10. Left Mc IV of an adult to senile lioness (SKMM No. 90/6528): cranial view.
Fig. 7 : Restes du crâne et de membres antérieurs de Panthera leo spelaea *(Goldfuss 1810) de grotte Keppler dans les montagnes karstiques du Sauerland (NO de l'Allemagne). 1. Mandibule droite d'une lionne adulte (SKMM No. 90/7047): vue latérale. 2. Mandibule gauche d'une femelle adulte (SKMM No. 90/7046): vue latérale. 3. Mandibule gauche d'un mâle adulte (SKMM No. 90/6495): vue latérale. 4. M1 droite d'une femelle adulte (SKMM No. 90/7048a): vue labiale. 5. M1 gauche d'une femelle adulte (SKMM No. 90/7048b): vue labiale. 6. Humérus droit d'un mâle adulte ou âgé (SKMM No. 90/6521): vue crâniale. 7. Humérus droit d'une femelle adulte ou âgée (SKMM No. 90/6520): a. vue crâniale, b. vue latérale droite, avec des stries de carnivores. 8. Humérus droit d'un mâle adulte ou âgé (SKMM No. 90/6522): vue crâniale. 9. Métacarpien IV gauche d'un mâle adulte ou âgé (SKMM No. 90/6531): vue crâniale. 10. Métacarpien IV gauche d'une femelle adulte ou âgée (SKMM No. 90/6528): vue crâniale.*

One pelvic fragment from the left side (fig. 9.1) is from an adult animal, whereas the acetabulum diameter width is 49 mm. Hind limb bones are present, all from adult animals, with two femora, one tibia and three metatarsi. The first right and distally larger male femur is proximally modern broken and chewed distally by carnivores (fig. 9.2a-c). One complete right femur is most likely from a large animal (fig. 9.3) with its 405 mm length and distal width of 60 mm. A complete left tibia (fig. 9.4) measures 355 mm in length and falls into the female size-range. The pedal skeleton is represented by a right mt II (fig. 9.5); a right mt III from with a chewed distal joint (fig. 9.6), and finally a left mt III from an adult to older animal (fig. 9.7).

3.7 - KREUZ CAVE MATERIAL

A right mandible of a grown up individual was found in unclear context and as single remain in the cave (fig. 7.1).

3.8 - MARTINS CAVE MATERIAL

The 17 bones were excavated in the hyena den cave near Lethmathe (Schaaffhausen, 1875) which are listed in table 3, and are figured here in most cases. A half P tooth (fig. 6.3) is the only cranial remain. The fore limb is preserved by a cracked and chewed ulna of a grown up animal (fig. 6.6), and several metacarpi (fig. 6.7 and 6.8). The axial skeelton has one incomplete middle caudal (fig. 6.11) and one lumbar vertebra preserved. The astragalus has bite damages (fig. 6.12), one astragalus is complete (fig. 6.13). The hind limb is represented additionally by five metatarsi (fig. 6.14, 6.15, 6.16, 6.17, 6.18 and 6.19). The phalangy I bones (fig. 6.20, 6.21 and 6.22) are unclear in their pedal positions, but one has bite damages.

3.9 - PERICK CAVES MATERIAL

The only nearly complete skull of a lioness was described with all bones figured monographically with a taphonomic discussion of the remains in a cave bear and hyena den (Diedrich, 2008b).

3.10 - PFEFFERBURG CAVE MATERIAL

From this hyena den, only a non-figured metapodial and one phalanx II are in the few today preserved historical collection.

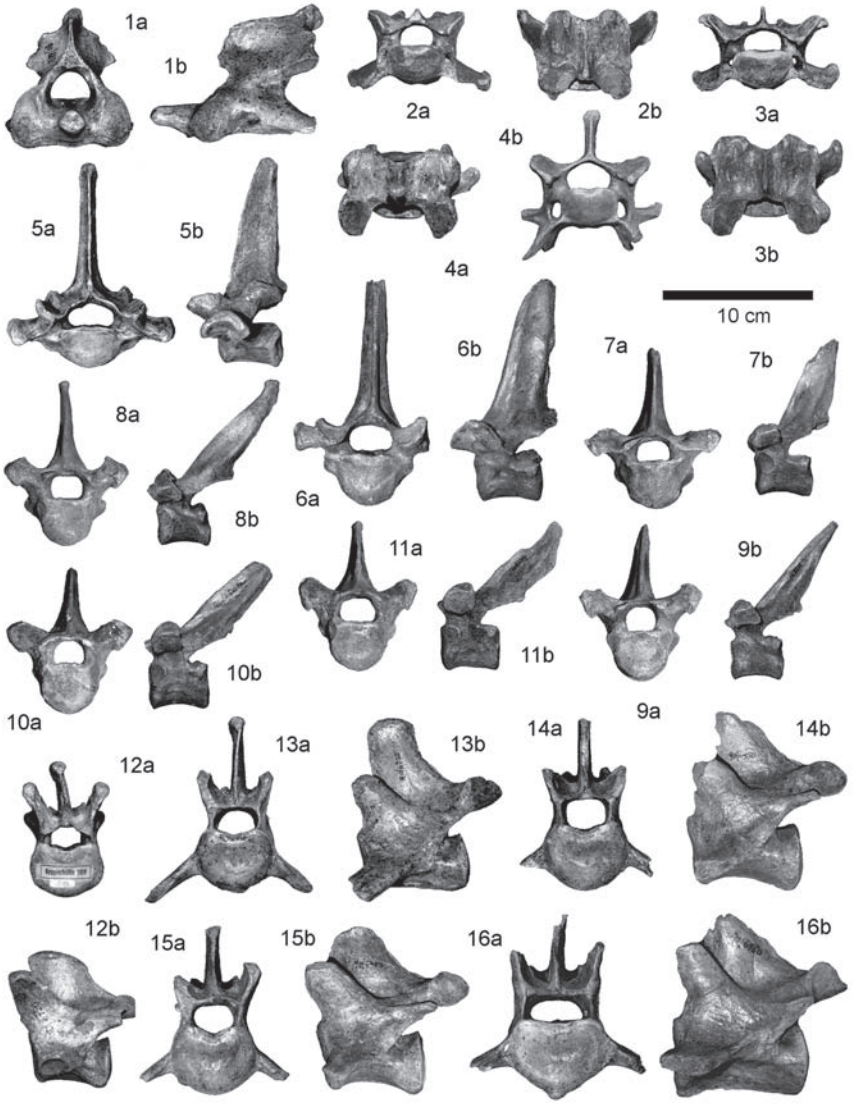


Fig. 8: ***Panthera leo spelaea*** **(Goldfuss 1810) vertebral column remains from Keppler Cave of the Sauerland Karst Mountains (NW Germany).** 1 Axes of an adult animal (SKMM No. 90/6273): a. cranial view, b. lateral left view. 2. C3 of an adult animal (SKMM No. 90/6799): a. cranial view, b. lateral left view. 3. C5 of an adult animal (SKMM No. 91/8751): a. cranial view, b. lateral left view. 4. C6 of an adult animal (SKMM No. 90/6754): a. cranial view, b. lateral left view. 5. T1 of an adult animal (SKMM No. 91/8752): a. cranial view, b. lateral left view. 6. T2 of an adult animal (SKMM No. 91/8753): a. cranial view, b. lateral left view. 7. T4 of an adult animal (SKMM No. 90/6795) a. cranial view, b. lateral left view. 8. T7 of an adult animal (SKMM No. 90/6806) a. cranial view, b. lateral left view. 9. T8 of an adult female (SKMM No. 91/8754) a. cranial view, b. lateral left view. 10. T9 of an adult animal (SKMM No. 91/8755) a. cranial view, b. lateral left view. 11. T10 of an adult animal (SKMM No. 91/8756) a. cranial view, b. lateral left view. 12. T14 of an adult animal (SKMM No. 91/8757): a. cranial view, b. lateral left view. 13. L3 of an adult animal (SKMM No. 90/6750): a. cranial view, b. lateral left view. 14. L5 of an adult animal (SKMM No. 91/8758): a. cranial view, b. lateral left view. 15. L5 of an adult animal (SKMM No. 91/8759): a. cranial view, b. lateral left view. 16. L6 of an adult animal (SKMM No. 91/8760): a. cranial view, b. lateral left view.
Fig. 8 : Restes de la colonne vertébrale de Panthera leo spelaea *(Goldfuss 1810) de la grotte Keppler dans les montagnes karstiques du Sauerland (NO de l'Allemagne). 1 Axis d'un animal adulte (SKMM No. 90/6273): a. vue crâniale, b. vue latérale gauche. 2. C3 d'un animal adulte (SKMM No. 90/6799): a. vue crâniale, b. vue latérale gauche. 3. C5 d'un animal adulte (SKMM No. 91/8751): a. vue crâniale, b. vue latérale gauche. 4. C6 d'un animal adulte (SKMM No. 90/6754): a. vue crâniale, b. vue latérale gauche. 5. T1 d'un animal adulte (SKMM No. 91/8752): a. vue crâniale, b. vue latérale gauche. 6. T2 d'un animal adulte (SKMM No. 91/8753): a. vue crâniale, b. vue latérale gauche. 7. T4 d'un animal adulte (SKMM No. 90/6795) a. vue crâniale, b. vue latérale gauche. 8. T7 d'un animal adulte (SKMM No. 90/6806) a. vue crâniale, b. vue latérale gauche. 9. T8 d'un animal adulte (SKMM No. 91/8754) a. vue crâniale, b. vue latérale gauche. 10. T9 d'un animal adulte (SKMM No. 91/8755) a. vue crâniale, b. vue latérale gauche. 11. T10 d'un animal adulte (SKMM No. 91/8756) a. vue crâniale, b. vue latérale gauche. 12. T14 d'un animal adulte (SKMM No. 91/8757): a. vue crâniale, b. vue latérale gauche. 13. L3 d'un animal adulte (SKMM No. 90/6750): a. vue crâniale, b. vue latérale gauche. 14. L5 d'un animal adulte (SKMM No. 91/8758): a. vue crâniale, b. vue latérale gauche. 15. L5 d'un animal adulte (SKMM No. 91/8759): a. vue crâniale, b. vue latérale gauche. 16. L6 d'un animal adulte (SKMM No. 91/8760): a. vue crâniale, b. vue latérale gauche.*

3.11 - WILHELMS CAVE MATERIAL

This cave was a hyena den only during the Upper Pleistocene, for which an individual skeleton remain of a young lion cub found in historic times (Hundt & Troschel, 1874) is remarkable (fig. 10). 15 bones are preserved, which show in some cases modern fractures. One upper jaw right canine is open from the root (fig. 10.1). From the fore limb both incomplete scapulae (fig. 10.2 and 10.3) are preserved, of which the left one consists only of the proximal part. The height of the right scapula is 222 mm. The right humerus measures 271 mm in length without its proximal joint. Both humeri are lacking its proximal joints. The right one has a fused distal joint, giving an individual age of a cub. The left humerus distal joint was broken modern. The vertebral column is

No.	Inv.-No.	Bone type	Commentary	Left	Right	Individual Age	Sex	Collection
1	90/7046	Mandible	Incomplete, Mandible height 51 mm M_1 length 33 mm, Posterior tip broken of during animals life	x		High adult to senile	Male	Stadtmuseum Menden
2	90/6495	Mandible	Incomplete, Mandible height 47 mm M_1 length 29 mm	x		Adult	Female	Stadtmuseum Menden
3	90/7047	Mandible	Incomplete, M_1 length 28 mm		x	Adult	Female	Stadtmuseum Menden
4	90/7048a	Tooth	M_1 length 27 mm		x	Adult	Female	Stadtmuseum Menden
5	90/7048b	Tooth	M_1 length 27 mm	x		Adult	Female	Stadtmuseum Menden
6	90/6520	Humerus	Complete, Length 342 mm Distal width 95 mm, with thin bite scratches		x	Adult	Female	Stadtmuseum Menden
7	90/6521	Humerus	Complete Length 360 mm Distal width 89 mm		x	Adult	Male	Stadtmuseum Menden
8	90/6522	Humerus	Complete Length 362 mm Distal width 8.5 mm		x	Adult	Male	Stadtmuseum Menden
9	90/6529	Metacarpus	Mc IV, Length 131 mm		x	Adult	Male	Stadtmuseum Menden
10	90/6531	Metacarpus	Mc IV, Length 121 mm	x		Adult	Female	Stadtmuseum Menden
11	90/6273	Cervical vertebra	Axes, incomplete			Adult	?Feale	Stadtmuseum Menden
12	90/6799	Cervical vertebra	C3, incomplete			Adult	?Female	Stadtmuseum Menden
13	91/8751	Cervical vertebra	C5, incomplete			Adult	?Female	Stadtmuseum Menden
14	90/6754	Cervical vertebra	C6, incomplete			Adult	?Female	Stadtmuseum Menden
15	91/8752	Thoracic vertebra	T1, complete			Adult	?Female	Stadtmuseum Menden
16	91/8753	Thoracic vertebra	T2, incomplete			Adult	?Male	Stadtmuseum Menden
17	90/6795	Thoracic vertebra	T4-5, incomplete			Adult	?Female	Stadtmuseum Menden
18	90/6808	Thoracic vertebra	T7, incomplete			Adult	?Female	Stadtmuseum Menden
19	90/8754	Thoracic vertebra	T8, incomplete			Adult	?Female	Stadtmuseum Menden
20	91/8755	Thoracic vertebra	T9, incomplete			Adult	?Female	Stadtmuseum Menden
21	91/8756	Thoracic vertebra	T10, incomplete			Adult	?Female	Stadtmuseum Menden
22	91/8757	Thoracic vertebra	T14, complete			Adult	?Female	Stadtmuseum Menden
23	90/6750	Lumbar vertebra	L3, incomplete			Adult	Male	Stadtmuseum Menden
24	91/8758	Lumbar vertebra	L5, incomplete			Adult	Female	Stadtmuseum Menden
25	91/8758	Lumbar vertebra	L5, incomplete			Adult	Male	Stadtmuseum Menden
26	91/8760	Lumbar vertebra	L6, incomplete			Adult	Male	Stadtmuseum Menden
27	90/6962	Pelvic	Acetabulum, joint diameter 49 mm	x		Adult	?Female	Stadtmuseum Menden
28	90/6357	Femur	Without proximal part, distal width 96 mm, with strong 4-6 mm wide bite scratches in distal joint spongiosa		x	Adult	Male	Stadtmuseum Menden
29	90/6524	Femur	Complete, length 405 mm proximal width 86 mm		x	Adult	Female	Stadtmuseum Menden
30	90/6525	Tibia	Complete, length 355 mm proximal width 60 mm	x		Adult	Male	Stadtmuseum Menden
31	90/6527	Metatarsus	Mt III, incomplete, distally chewed		x	Adult	Female	Stadtmuseum Menden
32	90/6530	Metatarsus	Mt III, length 145 mm pathology	x		Adult	Male	Stadtmuseum Menden
33	90/6526	Metatarsus	Mt II,length 122 mm		x	Adult	Female	Stadtmuseum Menden

Tab. 2: Bone list of *Panthera leo spelaea* (Goldfuss 1810) remains from the Keppler Cave in the Sauerland Karst Mountains (NW Germany) from the Heinrich 1919-1920 collection.
Tab. 2 : Liste des restes osseux de Panthera leo spelaea *(Goldfuss 1810) de la grotte Keppler dans les montagnes karstiques du Sauerland (NO de l'Allemagne), collection Heinrich 1919-1920.*

Fig. 9: ***Panthera leo spelaea*** **(Goldfuss 1810) hind limb remains from Keppler Cave of the Sauerland Karst Mountains (NW Germany).** 1. Left pelvic fragment of an adult to senile animal (SKMM No. 90/6962): lateral view. 2. Right femur of an adult to old lion with scavenged marks on the distal joint (SKMM No. 90/6357): a-c. cranial view. 3. Right femur of an adult to senile lioness (SKMM No. 90/6524): cranial view. 4. Left tibia of an adult to senile male (SKMM No. 90/6525): cranial view. 5. Right Mt II of an adult to senile lioness (SKMM No. 90/6526): cranial view. 6. Right Mt III of an adult to senile lioness with a chewed distal joint (SKMM No. 90/6527): a-b. cranial view. 7. Left Mt III of an adult to senile male (SKMM No. 90/6530): cranial view.
Fig. 9 : Restes de membres postérieurs de Panthera leo spelaea *(Goldfuss 1810) de la grotte Keppler dans les montagnes karstiques du Sauerland (NO de l'Allemagne). 1. Fragment pelvien gauche d'un animal adulte ou âgé (SKMM No. 90/6962): vue latérale. 2. Fémur droit d'un animal adulte ou âgé avec des traces de rognage sur l'articulation distale (SKMM No. 90/6357): a-c. vue crâniale. 3. Fémur droit d'une femelle adulte ou âgée (SKMM No. 90/6524): vue crâniale. 4. Tibia gauche d'un lion adulte ou âgé (SKMM No. 90/6525): vue crâniale. 5. Métatarsien II droit d'une femelle adulte ou âgée (SKMM No. 90/6526): vue dorsale. 6. Métatarsien III droit d'une femelle adulte ou âgée avec des traces de rognage distal (SKMM No. 90/6527): vue dorsale. 7. Métatarsien III gauche d'un lion adulte ou âgé (SKMM No. 90/6530): vue dorsale.*

No.	Inv.-No.	Bone type	Comment	Left	Right	Sex	Age	Collection
1	A5F1231a	Ulna	Distal half missing, cracked		x		Adult	GPI Münster
2	M2466	Metacarpus	Mc II, bite marks	x		Male	Adult	Goldfussmuseum Bonn
3	M2462	Metatarsus	Mc IV, bite marks	x		Male	Adult	Goldfussmuseum Bonn
4	A5F1231b	Lumbar vertebra	Incomplete, neural arch				Adult	GPI Münster
5	A5F1196	Caudal vertebra	Middle				Adult	GPI Münster
6	A5F1231	Calcaneus	Incomplete, bite marks		x		Adult	GPI Münster
7	M2460	Astragalus	Complete		x	Male	Adult	Goldfussmuseum Bonn
8	M2463	Metatarsus	Mt II, bite marks		x	Male	Adult	Goldfussmuseum Bonn
9	M2464	Metatarsus	Mt II, distal incomplete, bite marks		x	Male	Adult	Goldfussmuseum Bonn
10	M2470	Metatarsus	Mt III, bite marks		x	Male	Adult	Goldfussmuseum Bonn
11	M2470a	Metatarsus	Mt IV, bite marks		x	Male	Adult	Goldfussmuseum Bonn
12	M2462	Metatarsus	Mt IV, bite marks	x		Male	Adult	Goldfussmuseum Bonn
13	A5F280	Metatarsus	Mt V				Adult	GPI Münster
14	A5F1231b	Metatarsus	Mt V		x		Adult	GPI Münster
15	A5F1198	Phalanx I	Incomplete, bite marks				Adult	Goldfussmuseum Bonn
16	A5F1197	Phalanx I	Incomplete				Adult	Goldfussmuseum Bonn
17	A5F1185	Phalanx I	Complete				Adult	Goldfussmuseum Bonn

Tab. 3: ***Panthera leo spelaea*** **(Goldfuss 1810) bone remains from the Martins Cave (NW Germany).**
Tab. 3 : Restes osseux de Panthera leo spelaea *(Goldfuss 1810) de la grotte Martins (NO de l'Allemagne).*

represented by the axes (fig. 10.6) and the last lumbar vertebra No. 7 (fig. 10.7); both are missing the centrum discs. From the pelvic bone, the sacrum (width of 78 mm with the first two elements: fig. 10.8) is incomplete. Also here, the disc is missing. The rib cage is represented by three incomplete, middle thoracic ribs, two of them are from the right side (fig. 10.10 and 10.11), one costa is from the left thorax (fig. 10.9). The joint head discs are absent and were non-fused. The here-figured lion ribs were formerly mounted incorrectly in a hyena skeleton montage consisting mainly of hyena bones from this cave (Humpohl *et al*. (1997); there named "Biggethal Cave"). There are four hind limb bones: one right femur shaft 292 mm in length (fig. 10.12), both calcanei (length 106 mm each), without distal parts (fig. 10.13 and 10.14) and the right astragal (length 58 mm) are preserved (fig. 10.15).

3.12 - TEUFELSKAMMER CAVE MATERIAL

An incomplete small proportioned humerus from an early adult animal, which was cracked in the upper third

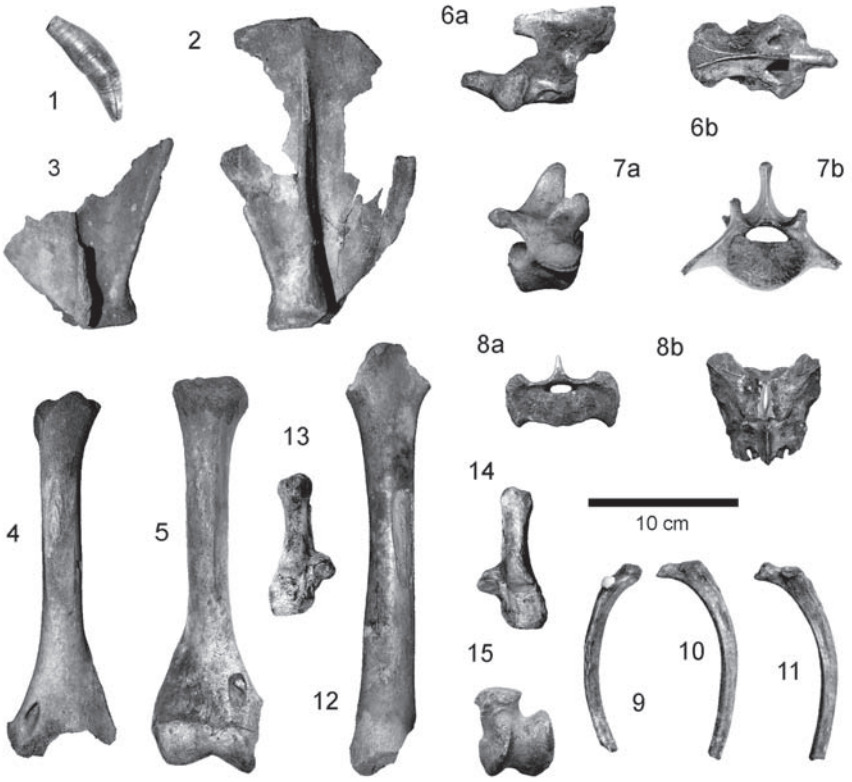


Fig. 10: Cub skeleton *Panthera leo spelaea* (Goldfuss 1810) remain from the Wilhelms Cave hyena den (NW Germany). 1. Right upper jaw canine (GPIM No. A5F1179): labial view. 2. Right scapula (GPIM No. A5102-1): lateral view. 3. Left scapula fragment (GPIM No. A5102-2): lateral view. 4. Left humerus (GMB No. M6006): cranial view. 5. Right humerus (GPIM No. A5F1180): cranial view. 6. Axes (GPIM No. A5F1298): a. lateral left view, b. dorsal view. 7. Last lumbar vertebra L7 (GPIM No. A5F1299): lateral right view, b. cranial view. 8. Sacrum (GPIM No. A5102-3): a. cranial view, b. dorsal view. 9. Middle left costa (GPIM No. A5F1225): caudal view. 10. Middle right costa (GPIM No. A5102-5): caudal view. 11. Middle right costa (GPIM No. A5F1088): caudal view. 12. Right femur shaft (GPIM No. A5102-4): cranial view. 13. Right calcaneus (GPIM No. A5F1262): cranial view. 14. Left calcaneus (GPIM No. A5F1263): cranial view. 15. Right astragal (GMB No. M792): dorsal view.
Fig. 10 : Squelette de jeune Panthera leo spelaea *(Goldfuss 1810) trouvé dans la tanière d'hyène de la grotte Wilhelms (NO de l'Allemagne). 1. Canine supérieure droite (GPIM No. A5102-1): vue latérale. 3. Fragment de scapula gauche (GPIM No. A5102 -2): vue latérale. 4. Humérus gauche (GMB No. M6006): vue crâniale. 5. Humérus droit (GPIM No. A5F1180): vue crâniale. 6. Axis (GPIM No. A5F1298): a. vue latérale gauche, b. vue dorsale. 7. Dernière vertèbre lombaire L7 (GPIM No. A5F1299): vue latérale droite, b. vue crâniale. 8. Sacrum (GPIM No. A5102 -3): a. vue crâniale, b. vue dorsale. 9. Côte intermédiaire (GPIM No. A5F1225): vue caudale. 10. Côte intermédiaire droite (GPIM No. A5102 -5): vue caudale. 11. Côte intermédiaire droite (GPIM No. A5F1088): vue caudale. 12. Diaphyse fémorale droite (GPIM No. A5102-4): vue crâniale. 13. Calcanéum droit (GPIM No. A5F1262): vue crâniale. 14. Calcanéum gauche (GPIM No. A5F1263): vue crâniale. 15. Astragale droite (GMB No. M792): vue dorsale.*

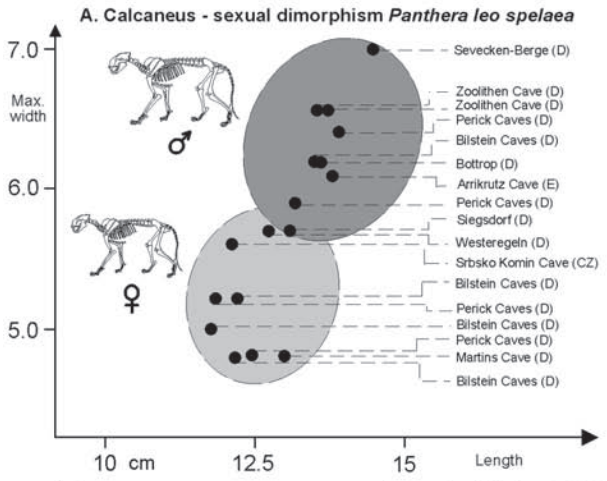
of the shaft, was chewed laterally at the distal joint by a large carnivore (fig. 6.4).

4 – DISCUSSION

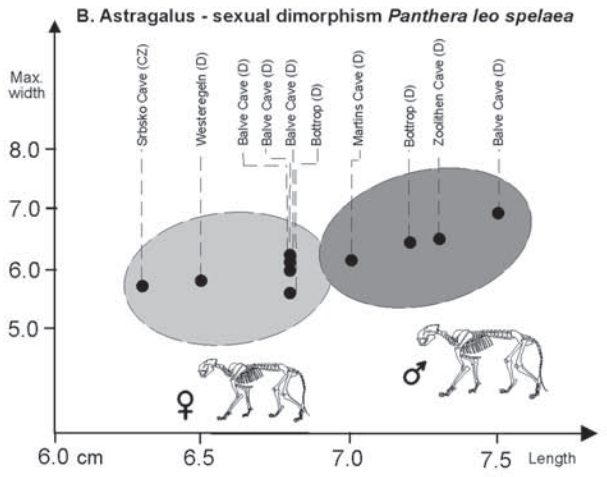
4.1 - THE BALVE CAVE LION POPULATION

The lion material was compared with other descriptions of European lions of the Middle to mainly Upper Pleistocene periods (cf. Heller, 1953; Dietrich, 1968; Schütt, 1969; Altuna, 1981; Turner, 1984; Argant, 1988; Gross, 1992; Guzvica, 1998; Baryshnikov and Boeskorov, 2001; Burger *et al*., 2004; Diedrich, 2004, 2007b, 2008a, 2009a, 2009c, 2009d, 2010b, 2010c, 2011c; Diedrich & Rathgeber, in press). Some metapodials from the Balve Cave are extremely large and seem to fit more to maximum-sized Saalian steppe lion remains compared to the descriptions of the few record of European material from the late Middle Pleistocene (Argant, 1988).

Anyway, here some of the Upper Pleistocene lion bones are compared in their proportions to other Middle European studied caves in Germany, and Czech Republic. Included are also a few data of Gross (1992), for which metric scheme was used. The few represented long-bone material of the Balve Cave was recently compared in another study of the Bilstein Cave, and Keppler Cave lions, two cave bear den sites in the Sauerland Karst without any human impact. Those caves are not far from the Balve Cave (see fig. 1). Also the Perick Cave material was used, which instead is from a cave bear and hyena den site. The lion long-bone data are not repeated here, because there is only one tibia in the Balve Cave material, which falls into the range of larger males (Diedrich, 2009d). Instead, other postcranial bones are compared statistically with Middle European caves, gypsum karst and open air hyena den sites by the calcaneus and astragalus (fig. 11A and 11B). The astragals of the Balve Cave might indicate a sexual dimorphism, whereas at least three of them seem to be smaller female ones, if all would be from cold periods and not from Eemian smaller sized



Calcaneus	Length	Maximal width
Sevecken-Berge (D)	14,30	7,00
Perick Caves (D)	13,60	6,40
Arrikrutz, skeleton (E)	13,50	6,10
Zoolithen Cave (D)	13,50	6,50
Zoolithen Cave (D)	13,30	6,50
Bottrop (D)	13,20	6,20
Bilstein Caves (D)	13,10	6,20
Siegsdorf, skeleton (D)	12,60	5,70
Perick Caves (D)	12,70	5,90
Martins Cave (D)	12,50	4,80
Westeregeln (D)	12,20	5,70
Perick Caves (D)	11,80	4,80
Bilstein Caves (D)	11,50	5,20
Bilstein Caves (D)	11,50	4,80
Srbsko Komin Cave, skeleton (CZ)	11,40	5,60
Perick Caves (D)	11,10	5,20
Bilstein Caves (D)	11,00	5,00



Astragal	Length	Maximal width
Balve Cave (D)	7,50	6,90
Zoolithen Cave (D)	7,30	6,50
Bottrop (D)	7,20	6,40
Martins Cave (D)	7,00	6,10
Bottrop (D)	6,80	6,00
Balve Cave (D)	6,80	6,20
Balve Cave (D)	6,80	6,10
Balve Cave (D)	6,80	5,60
Westeregeln (D)	6,50	5,80
Srbsko Komin Cave, skeleton (CZ)	6,30	5,70

Fig. 11. *Panthera leo spelaea* (Goldfuss 1810) sexual dimorphism comparisons of the hind limb bones. A. Calcaneus and B. Astragalus of German and Czech caves, gypsum karst and open air sites, nearly all identified as hyena dens (long bone comparisons in Diedrich (2009d); data in cm).
Fig. 11. Comparaison du dimorphisme sexuel de l'os du membre postérieur chez Panthera leo spelaea *(Goldfuss 1810). A. Calcanéum et B. Astragale comparaisons portant sur les grottes allemandes et tchèques, tant de karst gypseux que de sites de plein air, presque tous identifiés comme des tanières de hyène (comparaisons d'os longs dans Diedrich (2009d); données en cm).*

proportioned lions (Eemian lioness skeleton: Diedrich, 2010c) or if those are not from larger sized late Middle Pleistocene lionesses (Argant, 1988). One is in the uppermost range of males compared to cold period Weichselian/Würmian large lions (fig. 11B).

The lion material from the Balve Cave is not represented well enough to perform more detailed analyses. However, the material is still one of the four largest lion bone collections of the Sauerland Karst in Westphalia compared to the Perick Caves, Keppler Cave, Bilstein Caves, Wilhelms Cave and others (Diedrich, 2009a, 2009b, 2009d), and the only larger lion bone collection from a human influenced cave site of this region (sites: fig. 1). The early to middle Weichselian lion material of the Perick Caves hyena and cave bear den contain the only known, nearly complete, lioness skull (Diedrich, 2009a) of the Sauerland Karst. The Wilhelms Cave has produced skeleton remains from a lion cub, which hyenas must have been imported as kill into their den cave. As described for the Bilstein Caves (Diedrich, 2009d); the Keppler Cave herein has also delivered only adult lion material. All lion remains occur at all cave sites, that are hyena den caves and cave bear dens (cf. Diedrich, 2009b). Additionally to the material from other German and Czech localities, other material was integrated from the hyena den gypsum karst sites Thiede (Lower Saxony), Quedlinburg Sevecken-Berge and Westeregeln (Saxony-Anhalt), or material from the Zoolithen Cave (Bavaria), such as the skeleton find from the Czech Srbsko Cave (Bohemian Karst), and material from the Sloup and Výpustek Caves (Moravian Karst). Finally, from the Westphalian open air site Bottrop (fig. 1) proportions of bones were compared (fig. 11).

Eighteen female bones (58 %) and thrirteen male bones (42 %) can be identified in the Balve Cave material due to their noticeable size differences. All other bones are too incomplete, or represent intermediate sizes, which are difficult to use when attempting to identify the sex. In the Bilstein Cave, the lioness material (NISP = 38 bones; Diedrich, 2009d) dominates with 67 %. Keppler Cave lion material includes at least two lion and two lioness remains, all being from adult to senile individuals. The percentage of lionesses seems to be, with 22 bones (67 %) higher then lion remains (11 bones = 33 %). Juvenile or adolescent material is absent. In the Perick Caves, it is opposite, here 66 % are males and the rest are from females (NISP = 59 bones; Diedrich, 2009a). More caves, and especially hyena dens, must be studied in their lion bone content to form a theory about possible male or female lion dominance in cave sites.

4.2 - THE BALVE CAVE HYENA DEN

General human versus carnivore bone accumulation studies were tried to distinguish bone assemblages using actuopalaeontological comparisons (e.g. Cooper, 1993; Fosse, 1999; Pickering, 2002; Stiner, 2004; Lansing *et al*., 2007). New excavations at Balve Cave in future must focus on such taphonomic problems with the background knowledge of the multiple cave use by hyenas, cave bears and humans.

The Balve Cave was recently identified as a periodically used hyena den for at least the early to middle Weichselian period (Diedrich, 2011a). The criteria for the late Pleistocene hyena den and commuting site identifications are followed *sensu* Fosse (1999), Diedrich and Žák (2006), and Diedrich (2011d). After Kuhn *et al*. (2008) in modern hyena "accumulated bone assemblages" a high amount of bones with crenulated edges and punctures are present. This is also observed on the selected "incomplete bone material" of the Balve Cave, which can be referred in many cases well to Ice Age spotted hyena activities (Diedrich, 2011a). Another proof for a hyena den and commuting site at the Balve Cave is a relatively large amount of hyena *Crocuta crocuta spelaea* bone material including cannibalistic cracked hyena bones or jaws and cub remains or imported, strongly chewed megafaunal prey remains, especially from *Coelodonta antiquitatis* (Diedrich, 2011a). The woolly rhinoceros bones are in most cases strongly damaged in repeating ways as figured similar for many other hyena den and prey accumulation sites: Bad Wildungen Biedensteg open air hyena den and prey depot (Diedrich, 2006), Perick Caves hyena den and prey depot (Diedrich, 2005, 2009a), and several hyena den and prey depot caves in the Bohemian Karst (Diedrich & Žák, 2006). It is less the numeric analyses that support the hyena origin to distinguish from human sites; it is more the repeating similar incomplete bone damage including "nibbling sticks" (cf. Diedrich, 2006, 2011a; Diedrich & Žák, 2006).

As established, juvenile hyena remains of the Balve Cave (Diedrich, 2011a) are best indicators for "hyena bone accumulation proves" (cf. Kuhn *et al*. 2008), they are accepted well to be the indicators for hyena den sites (cf. Pickering, 2002). Those are recently known for the Pleistocene to indicate even the den type of a "cub raising den" (cf. modern: East *et al*., 1989; Pleistocene: Diedrich, 2006, 2011a; Diedrich & Žák, 2006). Such modern cub raising and protecting den sites are well-known for African spotted hyenas (e.g. Kruuk, 1972; Cooper, 1993; Frank, 1994; Estes, 1999). In contrast to those cub dens, their remains are mostly absent at "commuting or prey accumulation sites" (definitions for Pleistocene dens *sensu* Diedrich & Žák, 2006). Hyena remains are sometimes absent even at hyenid "bone accumulation sites" (cf. Kuhn *et al*., 2008).

Pickering (2002) and Kuhn *et al*. (2008) suggested in modern African spotted hyena bone assemblage analyses that horns and antlers are not indicative for hyena dens, which has to be discussed shortly for the Balve Cave antler remains. Hyenas collected dropped antlers. Humans also did it, but the antler preservations is different. Humans collected those for tool productions, therefore for more then 50 reindeer antler fragments of selective mainly larger male ones were found in the Balve Cave with no bite marks. It is less the antler presence in the hyena dens that indicates a hyena origin, than the repeated chewed basal remains hyena left also in the Balve Cave with some specimens of *Rangifer tarandus* and *Megaloceros giganteus* antler bases (Diedrich, 2011a). Wolves do not import such dropped antlers to caves, or do not chew strongly on them, which was also excluded for the Italian hyena den caves (Stiner, 2004).

4.3 - LION BONE PRESENCE AT HYENA AND CAVE BEAR DENS

About 250 lion bones of the Sauerland Karst Caves of north-western Germany are dominated by adult to senile lion remains (99 %). This supports the theory of the non-use of caves by lions as a "den" to raise their cubs in caves or cavities. They seem never to have used caves, and their occurrence in those caves is partly a result of the antagonism between Ice Age spotted hyenas and steppe lions (Diedrich, 2007a; 2011e), but also a result of cave bear killing and scavenging by lions (fig. 12), which seem to be present also in Keppler Cave cave bear den. Therefore, the lions were renamed from "cave lions" to "steppe lions" (Diedrich, 2008a).

Most lion remains in Balve Cave are from the hyena den times of the late Pleistocene. The import of lion carcasses into hyena den sites is not only suggested for the Sauerland Karst caves (Diedrich, 2009a), it is discussed for some Bohemian Karst hyena den and prey depot caves (Diedrich & Žák, 2006). The presence of many lion metapodials is common at several studied hyena den sites and can be explained partly by the selective importation of legs. Other lion bones were damaged by hyenas in the main eating zones around the scapula/humerus and pelvic/femur areas, as recently described for the lion material from the Perick Caves (Diedrich, 2009a; fig. 3). Hyenas mostly did not scavenge on pedal skeletons from any kind of megafaunal animal leaving hereby within ungulate prey, the lower legs remaining untouched in their dens (cf. Stiner, 2004; Diedrich & Žák, 2006; Diedrich, 2010a), but there are exceptions. The distal pedal parts of carcasses were mostly left from the imported prey legs, because of the small amount of meat and missing bone marrow (cf. Stiner, 2004; Diedrich, 2010a). Typically, hyenas leave at lion scavenge sites the cranial bones, lumbar vertebrae, distal or complete legs, such as those described for Perick Caves (Diedrich, 2009a). In Perick Caves, the lion bones were in several cases cracked (lower jaws), nibbled and chewed; similar strongly damaged are bones damaged from Martins Cave hyena den. Nearly no scavenging marks were found on the lion bones from Balve Cave, which is in contrast to the lion bones from Martins Cave, Keppler Cave, Bilstein Cave, and Perick Caves (cf. Diedrich, 2009a, 2009d, 2011d), where several bones have bite marks caused by a large predator, most probably hyenas. At least there are some elongated parallel 3-4 mm wide bite scratch marks on Balve Cave tibia, caused by a large carnivore. Possibly both occipital areas of Balve Cave skulls are missing parts because of carnivore activities; this is difficult to prove, but at least it is another proof of hyena activity. A similar preservation was found at a lion brain case of Perick Caves (Diedrich, 2009a).

The large Sauerland caves were occupied by two other large animals, hyenas and cave bears. Late Pleistocene lions were open steppe and forest predators, similar

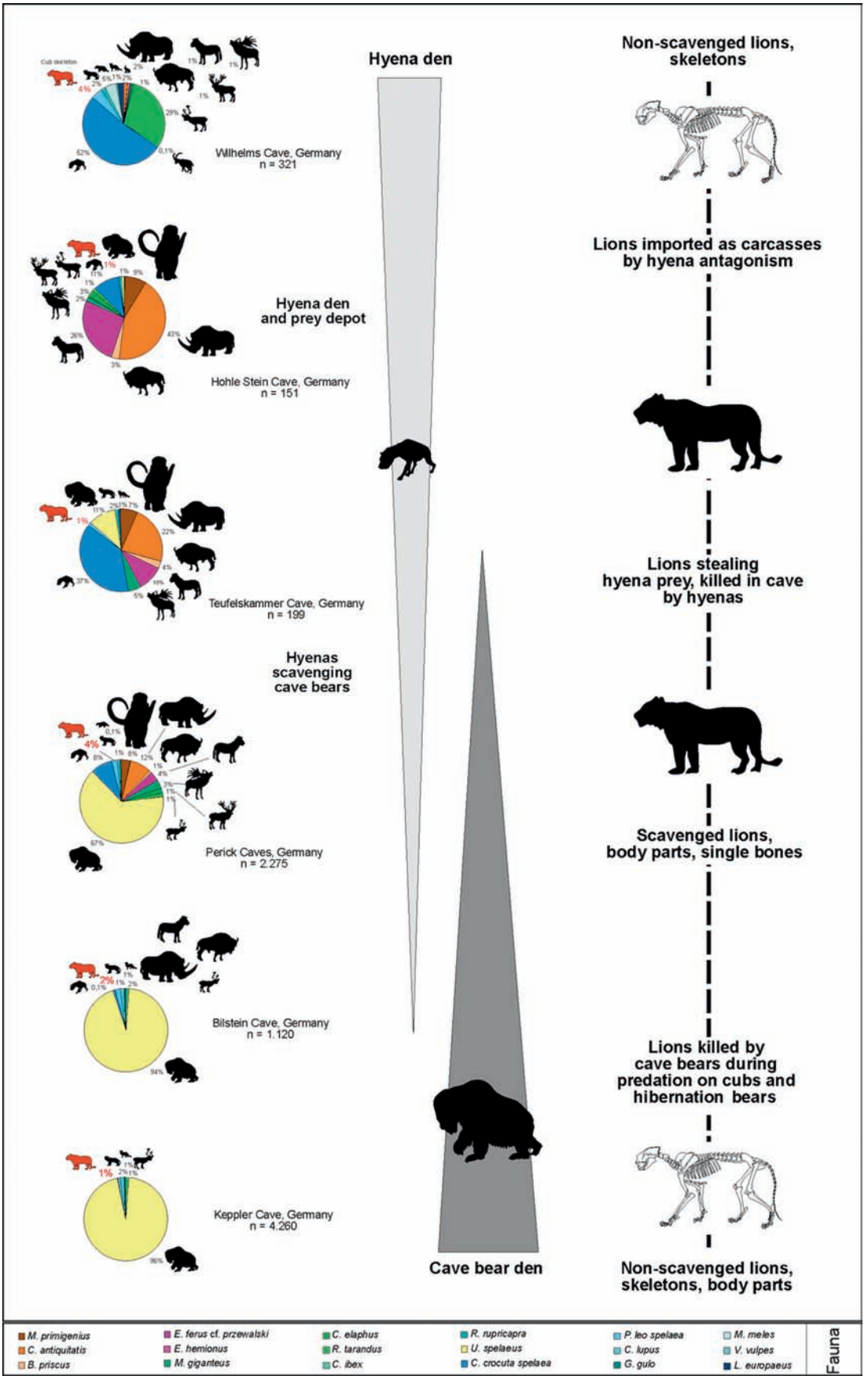


Fig. 12: Comparisons of *Panthera leo spelaea* (Goldfuss 1810) percentages (1-4 %) and carcass destruction stages in the most important non-human influenced Sauerland Karst hyena and cave bear den caves. The faunal statistics presents typical cave bear den and hyena den bone assemblages. The faunal percentages depend on the hyena impact and hyena prey importation.

Fig. 12 : Comparaison des pourcentages (1-4 %) et étapes de destruction des carcasses de Panthera leo spelaea *(Goldfuss 1810) dans les sites sans influence humaine les plus importants des grottes du karst du Sauerland de tanières d'hyène et de repaires l'ours. Les statistiques de faune représentent des assemblages typiques de tanière d'ours des cavernes et de tanières d'hyène. Les pourcentages de la faune dépendent de l'impact de l'hyène et de l'importation des proies par cette dernière.*

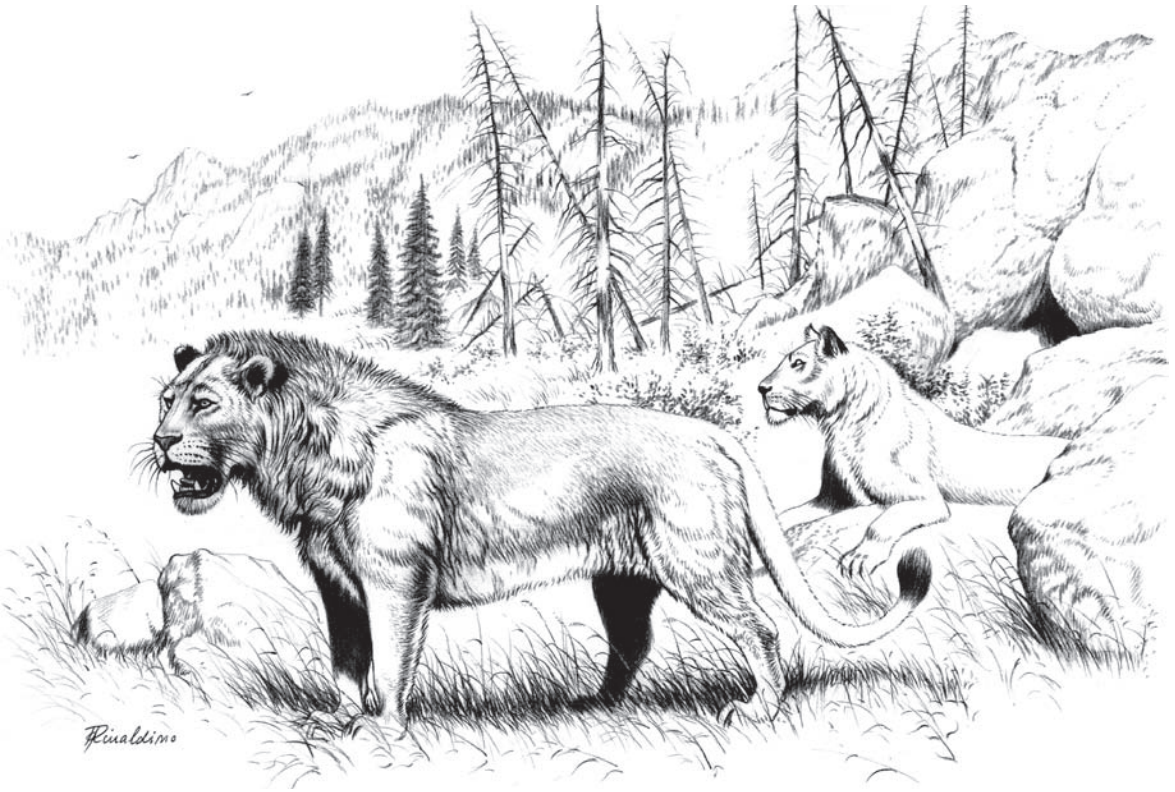


Fig. 13: *Panthera leo spelaea* (Goldfuss 1810) male with mane and typical tassel on the tail tip, and lioness in the background, in boreal forest environments of the Sauerland Karst Mountains (Illustration by G. "Rinaldino" Teichmann, 2010).
Fig. 13 : Panthera leo spelaea *(Goldfuss 1810) mâle avec crinière et houppe typique à la pointe de la queue, et lionne en arrière-plan dans les milieux de forêt boréale des montagnes karstiques du Sauerland (Illustration par G. Rinaldino Teichmann, 2010).*

to their modern relatives in Africa (Diedrich, 2007a, 2009a) and seem to have penetrated for two reasons the caves: (1) stealing hyenas their prey at the commuting or prey storage sites; or to kill their cubs in the raising cave sites as result of antagonism, and (2) for cave bear hunting (Diedrich, 2009a). In both cases antagonistic conflicts must be expected which caused the death of lions directly in caves. The Balve Cave, and the Keppler Cave material especially supports both theories that lions were killed by hyenas and possibly by cave bears in the caves, whereas Martins Cave material seem to have been imported by hyenas as carcass remains mainly (cf. Diedrich, 2009a).

In modern studies, information about lion or other large carnivore bone remains at hyena bone accumulations is poor. Only Lam (1992) and Pokines and Peterhans (2007) mentioned for few modern spotted hyena den sites a comparative proof for the importation of lion carcass remains. For the late Pleistocene studied bone-rich cave and open air sites, this possibility why steppe lions were found in European caves or at hyena dens coincidently was discussed (Diedrich, 2007a, 2007b, 2008a, 2009a, 2009b, 2009d, 2011e), but new articulated skeleton lion finds in a cave in Romania (Diedrich *et al*., 2009) proove again their presence even very deep in cave bear den caves, as most probable cave bear hunt conflict result.

It is known that modern African spotted hyenas do kill usually the weaker lionesses, but never the male lions (Sutcliffe, 1970; Estes, 1999; Joubert & Joubert, 2003). Those kills are for antagonistic reasons (Ford, 2005). Hyenas also possibly imported carcasses of dead lions that died a natural death or from intra-species fighting (Schaller, 1972; Palomares & Caro, 1999).

4.4 - LION BONE PRESENCE DUE TO HYENA AND CAVE BAR ANTAGONISM VERSUS HUMAN IMPORTATION

The comparison of lion remains at non-human influenced sites (Perick Caves, Keppler Cave, Bilstein Cave, Wilhelms Cave, and others in the Sauerland Karst (cf. fig. 1, 12) excludes evidence, even here in the Balve Cave, of the import of lions by humans. There are no cut marks at the Balve Cave on the lion bones, especially the most common metapods. A large amount of manus and pes skeleton elements is not proof of a lion "fur import by humans" following possible lion kills by humans. This taphonomic situation is important, because there still remains the question if humans hunted, killed and imported lions to their settlement and camp sites in the Middle Palaeolithic. Only the presence of lion bones does not prove this. This is demonstrated here for the Balve Cave; where hyena activity is responsible for the large amount of accumulated bones, similar to the non-human influenced hyena den Perick Caves (Diedrich, 2009a) or Srbsko Chlum Komin Cave (Diedrich & Žák, 2006). It is not yet proven whether lions or hyenas were hunted and killed by humans; both of which were the most dangerous

predators and antagonists for humans and to each others and to cave bears at that time in Central Europe, but conflicts also have to be expected.

5 - CONCLUSION

The lion *Panthera leo spelaea* (Goldfuss 1810) bone material presence in all northwest German Sauerland Caves originates of two main carnivore ecological situations, and can be excluded in the overlapping Balve Cave Palaeolithic site to be "imported prey of humans for meat or fur purposes". The Balve Cave was several times used as periodic hyena *Crocuta crocuta spelaea* (Goldfuss 1823) den. Therefore, some remains of lions, which have even bite damages, might reflect imported and consumed carcass remains by hyenas, such as demonstrated for the Perick Caves hyena den lion remains. Additionally, lions might have been killed at the hyena den Balve Cave site due to antagonistic conflicts about prey or cub protection or territory. Also lion-cub-killing and import of its carcass seem to be present at the Wilhelms Cave hyena cub raising den site. Finally, supporting the "lion-cave bear killing model" for European caves, as a result of the mammoth steppe fauna scarcity/absence in mountainous regions, lion remains are typically found in few percentages (1-3 %) in nearly all cave bear dens of Europe, such as the German Zoolithen Cave, Bilstein Cave, the Keppler Cave and the periodically used cave bear den Balve Cave.

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