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Late Pleistocene steppe lion *Panthera leo spelaea* (Goldfuss, 1810) footprints and bone records from open air sites in northern Germany – Evidence of hyena-lion antagonism and scavenging in Europe

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ABSTRACT

Bone remains and a trackway of *Pantheraichnus bottropensis* nov. ichg. ichnsp. of the Late Pleistocene lion *Panthera leo spelaea* (Goldfuss, 1810) have been recovered from Bottrop and other open air sites in northern Germany. Some of these bones are from open air hyena den sites. A relative high proportion of lion bones (20%) exhibit bite, chew or nibble marks, or bone crushing and nibbling caused by a large carnivore. Repeated patterns of similar bone damage have been compared to bone remains found at hyena dens in gypsum karst areas and cave sites in northern Germany. Ice Age spotted hyenas have been the main antagonists and the main scavengers on lion carcasses. The remains appear to have been imported often by hyenas into their communal dens, supporting the theory of strong hyena-lion antagonism, similar to the well documented antagonism between modern African lions and spotted hyenas. Most of the lion bones from the open air hyena den at Bottrop are probably a result of such antagonism, as are the rare remains of these carnivores found within large hyena prey bone accumulations along the Pleistocene rivers. The Emscher River terrace also has the largest quantity of hyena remains from open air river terrace sites in northern Germany. Their cub remains, and incomplete chewed prey bones from mammoths and woolly rhinoceroses, typical of hyena activity, underline the character of these sites as cub-raising and communal dens, where their prey was accumulated along the riverbanks in a similar manner to modern African hyenas.

1. Introduction

The Late Pleistocene lion "*Felis spelaea*", first described by Goldfuss (1810), was originally thought to have been a cave inhabitant (e.g. Goldfuss, 1810; Boule, 1906; Fischer, 1994) and bones from this "cave lion" were found in many caves all over Eurasia (e.g. Dawkins and Sandfort, 1900; Heller, 1953; Ballesio, 1975; Hülle, 1977; Altuna, 1981; Tichy, 1985; Argant, 1988; Guzvica, 1998; Baryshnikov and Boeskorov, 2001; Currant, 2004; Diedrich, 2007a,c, 2008a, 2009a,c,g, 2011a,b,d,e,f,g; Diedrich et al., 2009). The forgotten holotype skull of this last European lion, a diseased male from the Zoolithen Cave in Bavaria, southern Germany, has recently been described from the historical Rosenmüller collection housed in the Natural History Museum of the Humboldt University Berlin (Diedrich, 2008a, 2011d). A new common name "steppe lion" has been introduced for the Upper Pleistocene *Panthera leo spelaea* (Goldfuss, 1810) (Diedrich, 2008a). This is the only large *Panthera*-felid known from Eurasia during the late Pleistocene (Burger et al., 2004; Fig. 1) which was only occasional cave-dweller, living mostly in non-cave environments of the mammoth stppe and boreal forests of Central Europe, even giving birth and raising the cubs in the open air (Diedrich, 2008a, 2011d).

Records of late Pleistocene steppe lions outside cave environments are, however, quite rare in Europe. They include the middle Upper Pleistocene footprints from the Bottrop-Welheim open air site (Fig. 2) which are unique in the world, and recent reports of the first articulated skeleton parts and many isolated bones from several gravel pits (river terrace sites) in the Upper Rhine valley of southern Germany (Diedrich and Rathgeber, 2011). The only known articulated skeleton from northern Germany is of a diseased lioness, recently reported from the late Pleistocene interglacial Eemian elephant graveyard and shallow lake site at Neumark-Nord Lake I (Diedrich, 2010b,c, Fig. 3). In contrast to southern Germany, lion remains from gypsum/limestone karst, open air river terrace and loess localities in northern Germany are quite rare (Dietrich, 1968; Diedrich, 2004), and are described herein from only 40 bone remains, compared to about 600 bones recovered within caves, mainly from the Sauerland Karst (Diedrich, 2009a,c, Fig. 1) but also from the Harz Mountains (Fischer, 1994). The lion remains

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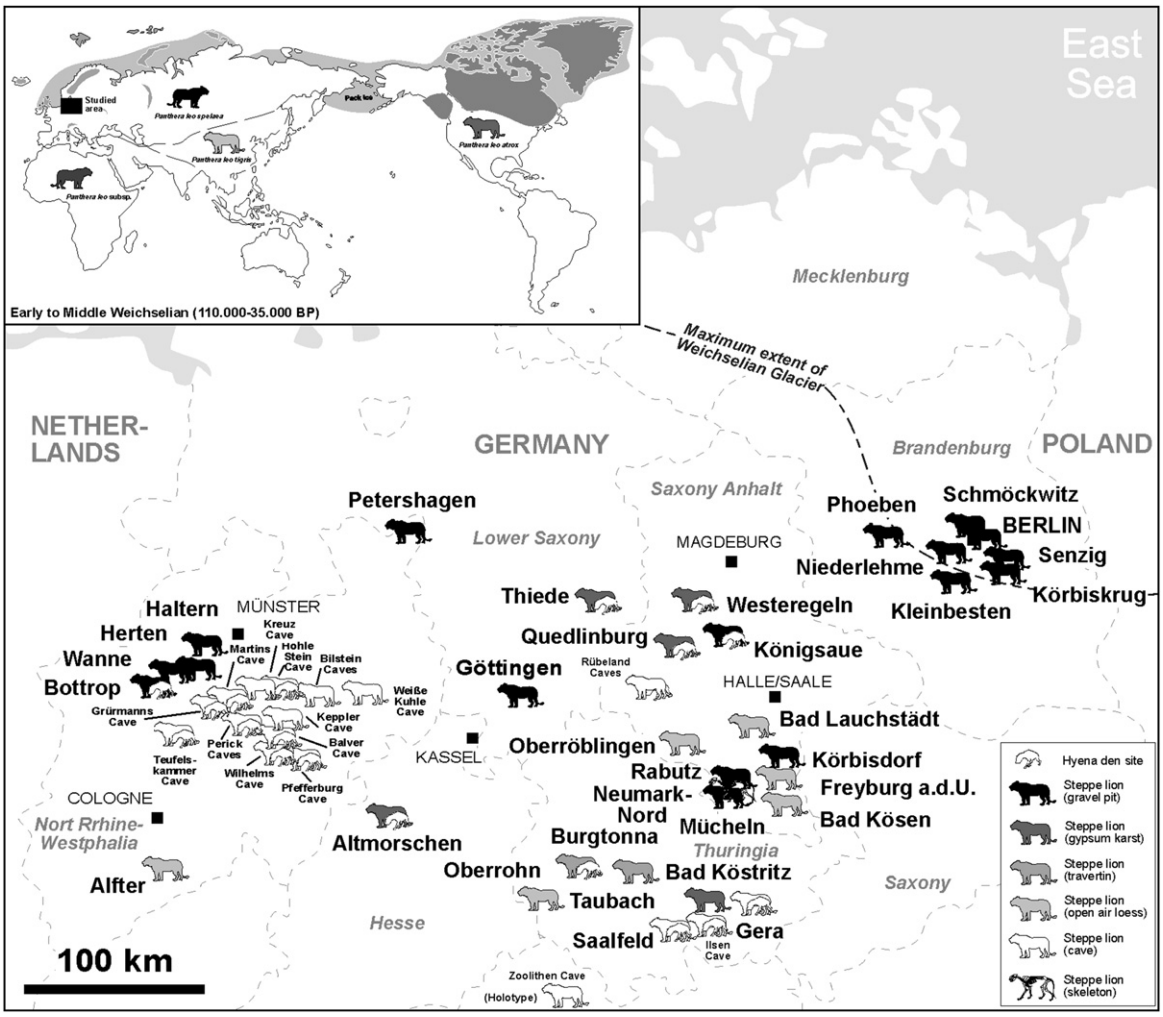

Fig. 1. Late Pleistocene steppe lion *Panthera leo spelaea* (Goldfuss, 1810) localities in northern and central Germany (compiled from new results and from Diedrich, 2004, 2008a, 2009a–c,e, 2010b,c; 2011b,d,g; Diedrich and Rathgeber 2011).

from three main gypsum and limestone karst sites at Thiede, Westeregeln and Quedlinburg (cf. Fig. 1), which are forgotten historical discoveries of Giebel (cf. Giebel, 1850a,b, 1852), and Nehring (Nehring, 1875, 1876, 1878a,b, 1890), have recently been rediscovered, and are included in this lion overview study in order to provide a broader analysis.

About 4.000 bones of Ice Age animals have been collected along the Emscher River near Bottrop (North Rhine-Westphalia, west-central Germany) between 1958 and 1976 "(Heinrich, 1983). These were mainly from non-carnivores and came from a three kilometre section of the Rhein-Herne-Kanal, and were collected from the surface of the "floating fields" (Heinrich, 1983, 1987). Several of the large mammoth and woolly rhinoceros bones have bite and chew marks typical of Ice Age spotted hyena scavenging activities. The 1.601 *Coelodonta antiquitatis* remains from Bottrop have demonstrated even furthermore a “slaughtering and carcass scavenging technique” by the Ice Age spotted hyenas *Crocuta crocuta spelaea*. Additionally several middle Palaeolithic Neandertal human artefacts have also been recovered, but without any stratigraphic context (Heinrich, 1983, 1987; Günther, 1988). These artefacts can not generally be related to the megafauna bones, as there is a complete absence of any cutting or striking marks on any of the larger bones. The bone accumulation along the Emscher River in Bottrop, instead, have been demonstrated to originate mainly of a hyena communal and cub-raising den and prey depot site type (Diedrich, 2011c).

Although a faunal list and the stratigraphy have been provided (Koenigswald and Walders, 1995; Frechen, 1995; see Fig. 2), only a preliminary listing was made of the lion bones which were compared in sizes to modern lions (Gross, 1992). These lion remains have been compared also to the Upper Pleistocene lion skeleton from an open air site, from Siegsdorf in southern Germany, which was found beside a mammoth skeleton (Gross, 1992). Cave bear remains from the Bottrop open air site have been recently discussed (Diedrich, 2009d), such massively chewed and damaged bones from mammoths and woolly rhinoceroses (Diedrich, 2011a, 2010a), all of which indicate this Bottrop terrace site to be one of the few recognized Upper Pleistocene open air communal hyena dens in northern Europe. The late Pleistocene bones in the Münsterland Bay Lowlands are generally found along the banks of ancient rivers, similar as in other open air hyena den, prey depot and cub raising sites, such as the loess site Bad Wildungen-Biedensteg, which was located close to a lake (Diedrich, 2006).

Lion remains have been found in various different taphonomic situations in northern Germany (Fig. 1), but only in Bottrop (North Rhine-Westphalia) has a larger quantity of remains found at open air river terraces. All other discoveries in gravel pits, from Wanne, Herten-Stuckenbusch, Haltern, and Göttingen, or around Berlin