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The recolonization of Europe by brown bears *Ursus arctos* Linnaeus, 1758 after the Last Glacial Maximum

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ABSTRACT

1. At the end of the Last Glacial Maximum brown bears *Ursus arctos* recolonized the glacial landscape of Central and Northern Europe faster than all other carnivorous mammal species of the Holocene fauna. *Ursus arctos* was recorded in Northern Europe from the beginning of the Late-Glacial. The recolonization of northern Central Europe may have taken place directly after the maximum glaciation. The distribution of the brown bear was restricted to glacial refugia only during the Last Glacial Maximum, for probably no more than 10 000 years.

2. Genetic analyses have suggested three glacial refugia for the brown bear: the Iberian Peninsula, the Italian Peninsula and the Balkans. Subfossil records of *Ursus arctos* from north-western Moldova as well as reconstructed environmental conditions during the Last Glacial Maximum in this area suggest to us a fourth glacial refuge for the brown bear. Because of its connection to the Carpathians, we designate this as the 'Carpathian refuge'.

3. Due to the low genetic distance between brown bears of northern Norway, Finland, Estonia, north-eastern Russia and the northern Carpathians (the so-called eastern lineage), the Carpathians were considered the geographical origin of the recolonization of these regions. During the recolonization of northern Europe the brown bear probably reached these areas rapidly from the putative Carpathian refuge.

Keywords: glacial refuge, Last Glacial Maximum, Late-Glacial, Post-Glacial, recolonization, subfossil record

INTRODUCTION

The first evidence for *Ursus arctos* in Europe is from the Middle Pleistocene (Chagneau & Prat, 1983). In subfossil deposits from the Late-Glacial and Holocene in Europe, the brown bear has been found in very large numbers (Sommer, Benecke & Kinzelbach, 2001). Its presence is described in many accounts of the faunal history of the Holocene (Noe-Nygaard, 1983; Lepiksaar, 1986; Ukkonen, 1993; Woodman, McCarthy & Monaghan, 1997; Benecke, 1999b,c; David, 1999; Kosintcev, 1999; Krakhmalnaya, 1999; McCormick, 1999; Mikkelsen *et al.*, 1999; Street & Baales, 1999; Yalden, 1999; Lõugas & Maldre, 2000). The recent distribution in Western Europe is strongly fragmented (Jacubiec, 1993). Based on the analysis of mitochondrial DNA, Taberlet & Bouvet (1994) produced a model for the postglacial recolonization of Europe by brown bears from glacial refugia. Zoogeographical suture zones were clearly visible (see Taberlet, Fumagalli & Wust-Saucy, 1998). In this study we attempt

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to reconstruct the late- and postglacial history of *Ursus arctos* distribution in Europe, based on subfossil records. Our results are compared with the genetic findings.

METHODS

From a large database containing zoological data from published and non-published archaeological reports from Europe (Benecke, 1999a), all available records of subfossil records of the brown bear from the Pleni-Glacial, Late-Glacial and Holocene were extracted. It was necessary to inspect and revise the data, to reflect the current attribution of subfossil finds to each time-period. For reference, all evaluated archaeological sites from Europe are listed by Sommer (2004).

Based on dating information, the data were grouped into chronozones (chz): chz. Ia Pleni-Glacial (75 000–15 000 BC), Ib Late-Glacial (15 000–9500 BC), II Pre-Boreal/Boreal (9500–7000 BC), III Atlantic (7000–5500 BC), IV Atlantic/Sub-Boreal (5500–3000 BC), V Sub-Boreal (3000–1000 BC), VI Sub-Atlantic 1 (1000 BC–0 AD), VII Sub-Atlantic 2 (0–600 AD) and VIII Sub-Atlantic 3 (600–1500 AD).

In most cases, subfossil bones were dated from their assignment to an archaeological layer. To get a precise temporal assignment of a record, ^{14}C dating of single bones was used. The ^{14}C-dating was taken directly from the literature or kindly made available by colleagues. Not all records could be grouped into chronozones, as in some cases they were dated unsuitably or inaccurately. In these cases, records were dated to only cultural epoch but were included in the investigation. For the classification of cultural epochs, the chronology of northern Europe was used. Using Geographic Information System (GIS), all finds from the different chronozones and cultural epochs were displayed sequentially on a digital map. All archaeological sites were mapped temporally and spatially, giving accurate data for the Late-Glacial and Post-Glacial distribution of *Ursus arctos*.

Individual finds (a point on a map) represent the remains of at least one individual from one archaeological site. A complete record of all investigated archaeological sites from the different chronozones is given by Sommer & Benecke (2004).

RESULTS

On the basis of subfossil assemblages the brown bear was recorded at 1268 different archaeological places and layers in Europe (Table 1). In the subfossil depositions of the Late-Glacial and Holocene in Europe the brown bear is, after the red fox *Vulpes vulpes*, the most frequently recorded carnivore.

Aside from 14 records from the Pleni-Glacial (Fig. 1, Table 1), mentioned among others by Altuna (1972), David (1999), Campbell (1977) and Zeuner (1953), the distribution of *Ursus arctos* can be traced in Europe until the Eemian Interglacial (Benecke *et al*., 1990). Many subfossil records are available from Ireland and Great Britain (Campbell, 1977; Hedges *et al*., 1996; Woodman *et al*., 1997; Currant & Jacobi, 2001), dated to the Hengelo-Deenekamp Interstadial before the maximum glaciation (*c*. 35 000–25 000 BC), based on numerous radiocarbon datings (Fig. 1).

In the Late-Glacial, the presence of the brown bear in Europe is shown by numerous subfossil records (Fig. 2) in Central Europe (Noe-Nygaard, 1983; Chaix & Olive, 1984; Altuna *et al*., 1991; Baales, 1994), as well as in Spain (Altuna, 1972), the British Islands (Campbell, 1977; Hedges *et al*., 1996; Woodman *et al*., 1997) and south-eastern Europe (Bolomey, 1973; Jullien, 1981). Bone remains from the British Isles with radiocarbon datings of 14 275 ± 120 BP, 12 378 ± 150 BP, 12 180 ± 130 BP, 11 920 ± 85 BP and 10 650 ± 100 BP (Campbell, 1977; Hedges *et al*., 1996; Woodman *et al*., 1997) show the presence of the brown

Table 1. Number of subfossil records of *Ursus arctos* in Europe from different epochs

Chronozone/cultural epoch	Records
Ia Pleni-Glacial (*c.* 75 000–15 000 BC)	15
Ib Late-Glacial (15 000–9500 BC)	39
II Pre-Boreal/Boreal (9500–7000 BC)	24
III Atlantic (7000–5500 BC)	46
IV Atlantic/Sub-Boreal (5500–3000 BC)	214
V Sub-Boreal (3000–1000 BC)	184
VI Sub-Atlantic 1 (1000 BC – 0 AD)	131
VII Sub-Atlantic 2 (0–600 AD)	97
VIII Sub-Atlantic 3 (600–1500 AD)	256
Mesolithic	24
Neolithic	58
Bronze Age	10
Iron Age/Roman Times	42
Migration Period	1
Middle Ages	8
Imprecisely dated/undated	108
Total	1257

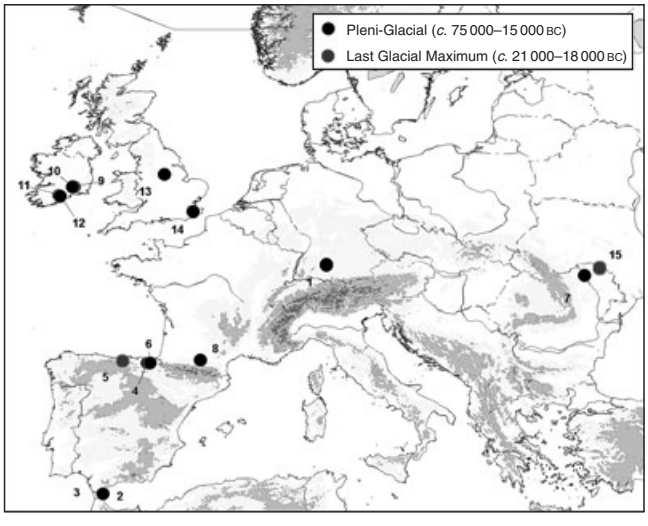

Fig. 1. Subfossil records of the brown bear in Europe from the Pleni-Glacial and Last Glacial Maximum, respectively. Legend: 1 Brillenhöhle, 2 Gorham's Cave, 3 Devil's Tower, 4 Leztxiki, 5 Cueva de El Castillo, 6 Cueva de Iruaxpe, 7 Duritor, 8 Cueva de Isturitz, 9 Shandon Cave, 10 Ballynamintra, 11 Castlepook Cave, 12 Foley Cave, 13 Robin Hood Cave, 14 Kents Cavern, 15 Cosauti.

bear in nearly all climatic epochs of the Late-Glacial. One of the important early records of *Ursus arctos* in Central Europe was found in the Kniegrotte Döbritz (Thuringia, south-eastern Germany). In this case the brown bear was a part of a faunal complex characteristic of a typical glacial fauna. Most of the radiocarbon datings of this faunal complex lie between 14 000 and 13 500 BC (Musil, 1974; Hedges *et al*., 1998; Höck, 2000). Further subfossil assemblages from Oelkenitz (Feustel, 1980; Hedges *et al*., 1998) and Teufelsbrücke (Feustel, 1980; Hedges *et al*., 1998), dated between the oldest Dryas and the Bølling, prove the presence of *Ursus arctos* during the early epochs of the Late-Glacial in that region (Fig. 2).

For the Post-Glacial brown bears are recorded in Scandinavia for the first time from the Pre-Boreal/Boreal (Iregren, Ringberg & Robertsson, 1990). The earliest proof of *Ursus arctos* in the Baltic States (Pulli, Estonia) is dated to the Pre-Boreal. This find was previously erroneously published as grey seal *Halichoerus grypus* (Lõugas 1997, 1999 and personal

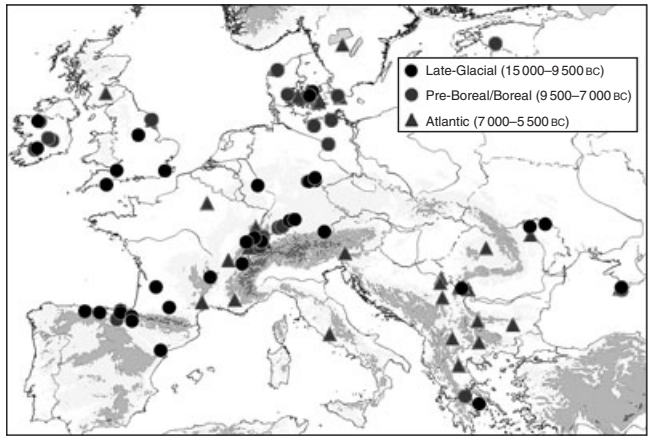

Fig. 2. Records of *Ursus arctos* from the Late-Glacial, Early and Mid-Holocene.

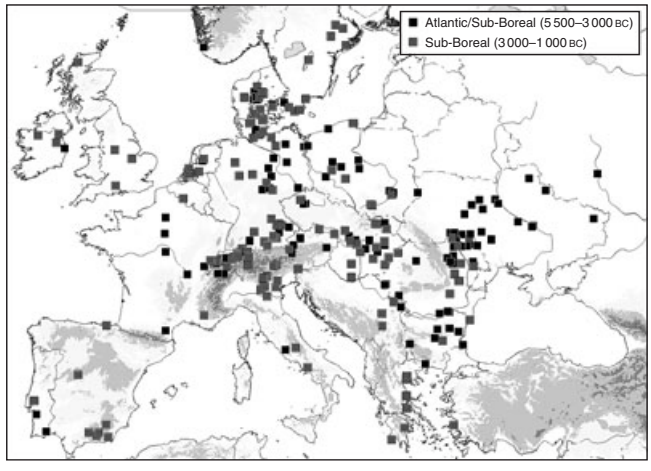

Fig. 3. Records of *Ursus arctos* from the late Atlantic and Sub-Boreal in Europe.

communication). Records from the early Atlantic are shown in Fig. 2. In this epoch the brown bear was recorded in bone finds from Italy (Rowley-Conwy, 1997), the Pannonic Basin (Clason, 1982) as well as the Carpathian Basin (El Susi & Rusu, 1995).

A remarkable increase in number and spatial distribution of records of *Ursus arctos* is visible during chronozone IV (5500–3000 BC), from the end of the Atlantic to the start of the Sub-Boreal period (Fig. 3). From that period evidence is known from Norway (Degerbøl, 1933), Poland (Necrasov & Haimovici, 1966; Schramm, 1987), the Donez-Dnepr area of the northern Ukraine (Gurin, 1992; Bibikova, 1963) as well as the southern part of the Urals in Russia (Petrenko, 1995). During the Sub-Boreal (3000–1000 BC) *Ursus arctos* is evidenced by Renouf (1989) in Finnmark, northern Norway (not mapped). An overview of all Sub-Boreal records is given in Fig. 3. A comprehensive collection of *Ursus arctos* remains is known from the different chronozones of the Sub-Atlantic (Fig. 4). Subfossil assemblages of the Sub-Atlantic 1 (1000 BC–0 AD) include records of the brown bear from the northern Caucasian foreland (Calkin, 1966) as well as from the Kama-Volga river region (not mapped in Fig. 4).

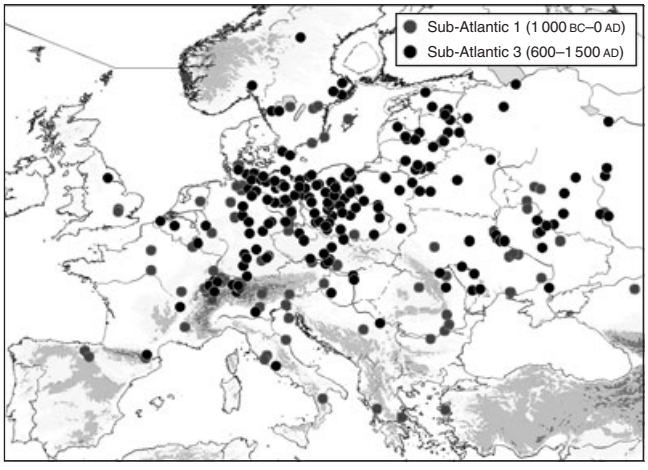

Fig. 4. Subfossil records of *Ursus arctos* in Europe from the chronozones Sub-Atlantic 1 and 3.

DISCUSSION

Recolonization of Europe in the Late-Glacial and Holocene

Based on numerous radiocarbon-dated bone remains, especially due to the record from Kents Cavern, which is almost concurrent with the beginning of the Late-Glacial, we can assume that *Ursus arctos* recolonized the glacial landscape, at least locally, directly following the retreat of the ice caps. We can conclude that under the influence of climatic change, the brown bear recolonized the area of Central Europe earlier than all other carnivorous mammal species of the 'typical' Holocene fauna.

The distribution of *Ursus arctos* was probably restricted to glacial refugia for less than 10 thousand years, during the coldest epoch of the Pleni-Glacial (25 000–15 000 BC). The precisely dated Late-Glacial records of the brown bear in Great Britain and Ireland (Fig. 2) are derived from geographical regions characterized (in contrast to Central Europe) by Arctic vegetation until the early Holocene (Lang, 1994). It is legitimate to assume the same degree of adaptability in brown bears from Central Europe and Scandinavia. Based on this high level of adaptability, the crossing of the Danish-Swedish land bridge to Scandinavia had probably already taken place during the earliest opportunity (Björck, 1996) during the Allerød.

In contrast to many forest-bound faunal elements, the well-adapted brown bear probably survived the very cold epoch of the youngest Dryas in southern Sweden. This area was cut off from the European mainland between *c.*10 800–10 000 BC due to the flooded Oresund Channel to the south and was bordered by ice caps to the north (Björck, 1996). Well-dated subfossil records of *Ursus arctos* in the north-western part of Europe show very early recolonization of the ice-free regions. It seems to be legitimate to conclude that the process of recolonization during the Late-Glacial was similarly efficient in other regions of Europe too. Because of that further discussion of the early Holocene records would seems unnecessary. All important records of the Middle Holocene until 1500 AD are mapped in Figs 2 and 3.

Glacial refugia

Due to the proven adaptability of *Ursus arctos* to the glacial climate, only records dated to the Last Glacial Maximum of the Pleni-Glacial are usable references for a glacial refuge. The references have to be based on an absolute dating of bone remains of the brown bear and an absolute dating of the analogical layer by radiocarbon dating. Among the Pleni-Glacial assemblages in Europe only two localities in Moldova (David, 1999; David *et al.*, 2003) are concordant with this specification (Fig. 1).

In such situations, it is advantageous to use the genetic data by Taberlet & Bouvet (1994) and Taberlet *et al.* (1998) for completion of that information. It is possible to detect three different glacial refugia from their data: (i) the Iberian Peninsula (Spain), (ii) the Italian Peninsula and (iii) the Balkans (Bulgaria/Greece). Furthermore, the investigation into the mitochondrial DNA of brown bears in Europe (Taberlet & Bouvet, 1994) shows four main points:

1. The individuals of southern Scandinavia originated from the Iberian Peninsula are closely related to the individuals from the Balkans and the Italian Peninsula, and form a 'western lineage'.

2. The bears of northern and eastern Scandinavia, from the Baltic States, from north-western Russia and the Carpathians differ with a sequence divergence of 7.13% from those individuals in the western lineage (Fig. 5).

3. Based on their genetic similarity, the brown bears from northern and eastern Scandinavia, the Baltic States, and north-western Russia are designated as 'eastern lineage' and a glacial refuge in eastern Europe is assumed to be the origin of this genotype (Hewitt, 1999).

4. Within the mitochondrial DNA of brown bears from the Carpathians, three different genotypes can be identified, whereas the genotype of bears from north of the Carpathians (Slovakia) is distributed throughout bears from Norway, Finland, the Baltic States and north-western Russia (Fig. 5).

Based on the subfossil record of *Ursus arctos* in Moldova, we conclude that this region was part of a glacial refuge of the brown bear, which was directly connected with the Carpathians by forest refugia (Zagwijn, 1992). Because of that, we name it the 'Carpathian refuge'. Besides the subfossil records, there are further clues that indicate a Carpathian refuge for the brown bear. Firstly, the area of the Pleni-Glacial records belongs to a region that was a forest refuge during the Last Glacial Maximum (Zagwijn, 1992). This forest refuge extended through northern Moldova into areas around the Carpathians. Secondly, the subfossil records in this region indicate the presence of various other, more forest-bound species during the maximum glaciation (David, 1999; David *et al.*, 2003; Sommer & Benecke, 2004). A glacial refuge for forest-bound animals in the Carpathians was acknowledged recently by numerous archaeozoologists and geneticists (I. Horaček, personal communication; P. Kotlik, personal communication; A. Nadachowski, personal communication; Hewitt, 2000; Sommer & Benecke, 2004; Deffontaine *et al.* 2005).

Based on the genetic findings of Taberlet & Bouvet (1994) (Fig. 5) and our own data, we assume that the recolonization of northern and eastern Scandinavia, the Baltic States and north-western Russia started from the Carpathians and the geographical origin of the so-

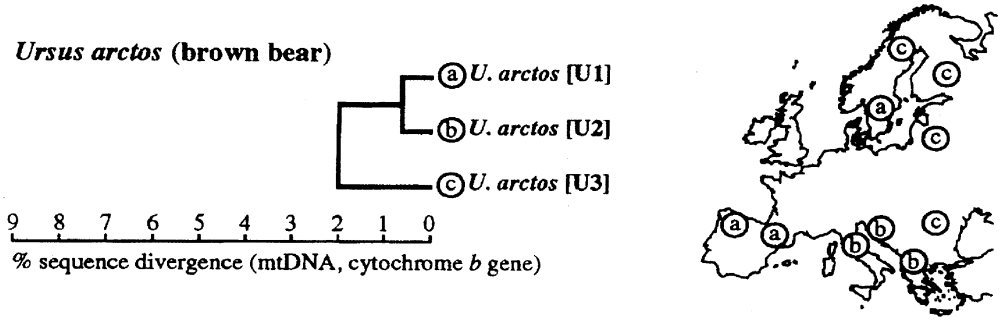

Fig. 5. Simplified phylogeography of *Ursus arctos* (reproduced with permission from Taberlet *et al.*, 1998).

called 'eastern lineage' is the Carpathian refuge. From the Carpathian region, the most northerly glacial refuge in Europe, it was possible for brown bears to recolonize areas of northern Europe very quickly. It also seems to be possible that the Crimean Peninsula was a glacial refuge of the brown bear. Besides numerous subfossil records of *Ursus arctos* from the Palaeolithic (Krakhmalnaya, 1999) as well as from the Late-Glacial (Benecke, 1999b), during the Pleni-Glacial the fauna of the Crimean shows a composition of typical Holocene and typical Pleistocene mammal fauna (Benecke, 1999b). Furthermore, the vegetation during the maximum glaciation in the Crimea, characterized by mixed forests (Zagwijn, 1992), was suitable for the survival of *Ursus arctos*. Unfortunately, the mammal assemblages of the Pleni-Glacial in the Crimea are not dated precisely enough. A comparison of mitochondrial DNA would be only possible from subfossil material, as the brown bear is extinct in this region.

CONCLUSIONS

The brown bear had a wide tolerance of the Pleni-Glacial and Late-Glacial climate. Its distribution during the Late-Pleistocene in Europe is indicated by numerous subfossil assemblages. Subfossil records from the Pleni-Glacial, accurately dated by radiocarbon dating, clearly show their presence in Central Europe during the Hengelo-Deenekamp Interstadial (*c*. 35 000–25 000 BC), the last warmer epoch of the Pleni-Glacial. After the maximum glaciation, *Ursus arctos* was present in north-western Europe by around 15 000 BC, the beginning of the Late-Glacial. The brown bear was already distributed in Central Europe during all colder and warmer phases of the Late-Glacial between 15 000 BC and 9500 BC. With the beginning of the Late-Glacial, *Ursus arctos* recolonized the glacial landscape, at least in local areas, directly following retreat of the ice caps. Under the influence of climatic change, the brown bear recolonized the area of Central Europe earlier than all other carnivorous mammal species of the 'typical' Holocene fauna.

The distribution of *Ursus arctos* was restricted to glacial refugia for probably less than 10 thousand years, directly during the coldest epoch of the Pleni-Glacial (25 000–15 000 BC). During this time, it was restricted to at least four different glacial refugia: the Iberian Peninsula, the Italian Peninsula, the Balkans and the Carpathians (including north-western Moldova). It also seems possible that the Crimean Peninsula may have been a glacial refuge of the brown bear. The recolonization of northern and eastern Scandinavia, the Baltic States and north-western Russia probably started from the Carpathians, and the geographical origin of the so-called 'eastern lineage' of the brown bears is the Carpathian refuge.

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