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THE LATE PLEISTOCENE HISTORY OF THE BROWN BEAR *URSUS ARCTOS* LINNAEUS, 1758 IN THE CZECH REPUBLIC

Adrian Marciszak[1]* • Jan Wagner[2] • René Kyselý[3] • Lena Matyaszczyk[1] • Martina Roblíčková[4] • Aleš Plichta[4,5] • Vlastislav Káňa[6]

[1]Department of Palaeozoology, University of Wrocław, Sienkiewicza 21, 50-335 Wrocław, Poland
[2]Department of Palaeontology, National Museum, Václavské náměstí 68, 110 00 Prague 1, Czech Republic
[3]Institute of Archaeology of the Czech Academy of Sciences, Prague, v.v.i., Letenská 4, 118 01 Prague 1, Czech Republic
[4]Anthropos Institute, Moravian Museum, Zelný trh 6, 659 37 Brno, Czech Republic
[5]Department of Geological Sciences, Faculty of Science, Masaryk University, Kotlářská 267/2, 611 37 Brno, Czech Republic
[6]Muzeum Blanenska p. o., Zámek 1, 678 01, Blansko, Czech Republic

ABSTRACT. During the Late Pleistocene (MIS 5e-2), the brown bear *Ursus arctos* was widespread in the Czech Republic. From this time interval, the species was recorded in 51 Czech localities, including 10 open-air and 41 cave sites. A total of 18 radiocarbon dates obtained from the material showed the presence of the species in this territory 46–12.6 kyr ago during the Late Pleistocene, but most of the dates are concentrated between 45.7 and 29.3 kyr. Later, its occurrence continued into the Holocene. Three dates confirmed the presence of *U. arctos* just before and during the LGM. However, during the coolest part of the GS-2.1b interval (about 20.9–19.0 kyr), the species was not recorded in the territory of the Czech Republic. A large, broad-toothed, highly carnivorous priscus ecomorph adapted to live in open grasslands occurred during the Late Pleistocene, while the arctos ecomorph was rarely recorded from that period. The post-LGM time (17.5–14.7 kyr) was characterised by increasing numbers of brown bear dates on the territory of the Czech Republic. It was also a period of progressive afforestation and the disappearance of the priscus ecomorph. The latest occurrence of the priscus ecomorph in the territory of the Czech Republic was represented by a robust mandible from the Býčí skála Cave, dated at 15.4–14.9 kyr.

KEYWORDS: Czech Republic, ectomorph, Late Pleistocene, occurrence, radiocarbon.

INTRODUCTION

Brown bear *Ursus arctos* Linnaeus, 1758 is a Holarctic species distributed across boreal, montane, arctic, forest, and open environments in almost all over the Northern Hemisphere. Over this wide area, this carnivoran exhibits a huge variability in ecology, genetics, behavior, and morphology (e.g., Erdbrink 1953; Baryshnikov 2007; Haroldson et al. 2020 and references therein; Swenson et al. 2020). This species is well adapted to cold environments with dense pelage, large fat stores, adaptability to various food sources, and the ability to reduce energy expenditure during winter by decreasing metabolism because of hibernation. Survival skills of the brown bear are some of the highest among all the carnivores, and this gives it great adaptability, an enormous ecological tolerance, and the capability to occupy different habitats; thus, today, this species is widespread in the Holarctic. Due to such a wide distribution, the brown bear is highly polymorphic; therefore, it has been split into a number of subspecies based on phenotypic differences (see Erdbrink 1953 and Baryshnikov 2007 for a review). The same results were obtained during the study of fossil materials. Because of the impossibility of collecting genetic information on older bones, morphological analyses are often the only approach that can be used to study the evolutionary lineage of the brown bear. However, this normally entails difficulties in defining and estimating intra- and interspecific variability, both chronologically and

*Corresponding author. Email: adrian.marciszak@uwr.edu.pl

geographically. Recent studies have shown the continual presence of *U. arctos* in Europe, even during the coldest periods of the Late Pleistocene (Sommer and Benecke 2005; Valdiosera et al. 2008; Davison et al. 2011; Edwards et al. 2014; Ersmark 2016; Ersmark et al. 2019; Marciszak et al. 2019). There were no sufficient natural barriers for brown bear dispersion, and its continuous gene flow across most of the European territory was observed during that time (Ersmark et al. 2019).

Despite that, in the last two decades, knowledge about the Pleistocene history of *U. arctos* in Europe has significantly increased, and there are still many countries where this topic is still relatively weakly known. Traditionally, the area of the Czech Republic is considered abundant in the ursid remains of the Late Pleistocene (Musil 1980; Wagner 2001; Kyselý 2005). Fossil lists are constantly supplemented and modified by new discoveries, both in the field and in collections, by rediscovering old fossils believed to be lost. Additionally, new dating and other analytic methods improve our knowledge about biochronology and provide new palaeobiological insights into the studied species and populations. Here, we present a new series of AMS dates obtained for the Late Pleistocene remains of *U. arctos* from the Czech Republic. The obtained dates are discussed in a wide biochronological and palaeoecological context.

SAMPLES AND METHODOLOGY

For the new dating, selected bones of *U. arctos* were pre-screened for their whole nitrogen content (Table 1). All 16 new radiocarbon dates (AMS) presented in this paper (see Table 1 for specimen information) were made in the Poznań Radiocarbon Laboratory (Poland), following their pre-treatment protocol for the extraction of collagen (Longin 1971; Piotrowska and Goslar 2002). Before extraction, the degree of collagen degradation was checked by measuring the nitrogen and carbon content in the bone using the analyser Flash EA 1112 Series (Thermo Scientific). The samples were regarded to be suitable for collagen dating if the nitrogen content was not lower than 0.6%, and C/N ratio was not higher than 5. Suitable bone fragments were crushed mechanically to granulation < 0.3 mm. The bone powder was then treated with 2M HCl (room temp., 20 min), and 0.1M NaOH (room temp., 1 hr). The sample was centrifuged, and the residuum was collected after each step of treatment. The extraction of collagen was processed in HCl (pH $= 3$, 80°C, 10 hr), and the residuum was removed after centrifugation. The extracted collagen was then ultra-filtered using pre-cleaned Vivaspin 15 MWCO 30 kD filters. The quality of collagen is ultimately assessed based on the C/N atomic ratio (interval of acceptance: 2.7–3.5) and collagen extraction yield (acceptance threshold: 0.5%). The carbon and nitrogen stable isotopic composition of collagen can be determined on demand (Bronk Ramsey et al. 2004). All new dates were calibrated using the program IntCal 20 according to Reimer et al. (2020). Within the text, only calibrated data were used.

Specimens with inventory numbers starting with NM are housed in the National Museum, Prague. The infraspecific nomenclature and taxonomy of Late Pleistocene brown bears (*U. arctos*) is rather confusing, as is also the case for their recent counterparts. Traditionally, but not unreservedly, the last glacial brown bears from Europe were assigned to a separate subspecies, *U. a. priscus* Goldfuss, 1818. Its phenotypic peculiarities were mostly based on specimens from periglacial areas (e.g., Thenius 1956; Musil 1964). The situation becomes confusing when Pacher (2007) revised the holotype of *U. a. priscus* and found that this skull looks very recent and does not bear morphological characteristics traditionally associated with *U. a. priscus*. Moreover, some other subspecies were described

Table 1 Radiocarbon dates of the Late Pleistocene *Ursus arctos* remains from Czechia.

No.	Site	Lab code	^{14}C age	Cal BP 95.4%	Bone	Coll. No.	% coll.	N	C	%N	%C	C:N	Source
1.	Praha-Řeporyje	Poz-86744	10790 ± 60	12836–12689	Mandible	NM-R 5504	1.6	1.1	5.0	14.9	41.9	3.3	This paper
2.	Pekárna Cave	Poz-86791	12610 ± 60	15231–14821	Mandible	NM-R 189	2.3	0.9	4.2	12.6	35.8	3.3	This paper
3.	Býčí skála Cave	Poz-86792	12730 ± 60	15363–14981	Mandible	NM-R 59	1.2	0.9	6.5	15.1	42.3	3.3	This paper
4.	Jáchymka Cave	Poz-89020	12790 ± 80	15552–15037	Mandible	—	0.1	0.7	3.8	—	—	—	This paper
5.	Hadí Cave	Poz-86800	12840 ± 50	15550–15168	Mt II	NM-R 199	3.0	1.2	6.6	13.1	34.9	3.1	This paper
6.	Praha-Bohdalec	Poz-86751	18590 ± 110	22885–22321	Skull	NM-R 1916	2.9	1.1	5.5	14.1	41.2	3.4	This paper
7.	Praha-Břevnov	Poz-86743	19270 ± 110	23412–22961	Humerus	NM-R 6210	7.2	3.2	9.8	15.1	42.1	3.3	This paper
8.	Pod Hradem Cave	OxA-30136	21940 ± 140	26445–25907	—	—	—	6.9	19.5	—	—	—	Ersmark et al. 2019
9.	Předmostí	—	25350 ± 130	29956–29246	—	—	—	—	—	—	—	—	Ersmark et al. 2019
10.	Praha, Svatoprokopská Cave	Poz-86741	27550 ± 260	31997–31117	Maxilla	NM-Ra 1042	5.4	3.2	9.8	15.8	45.0	3.3	This paper
11.	Martina Cave	Poz-80462	28020 ± 410	33283–31197	Ulna	NM-Rv 20650	0.2	0.8	4.2	—	—	—	This paper
12.	Martina Cave	Poz-86748	28110 ± 280	33136–31506	Ulna	NM-Rv 20650	0.3	0.9	4.5	18.4	52.8	3.4	This paper
13.	Martina Cave	Poz-86749	34400 ± 500	40845–38151	Radius	—	0.4	0.5	4.0	12.2	34.4	3.3	This paper

(Continued)

Table 1 (*Continued*)

No.	Site	Lab code	^{14}C age	Cal BP 95.4%	Bone	Coll. No.	% coll.	N	C	%N	%C	C:N	Source
14.	Nad Kačákem Cave	Poz-86803	34600 ± 400	40746–39067	Humerus	NM-Rv 21437	6.2	2.3	8.3	14.1	42.3	3.5	This paper
15.	Vavřinecké paleo-ponory Cave	Poz-86753	34600 ± 600	41127–38147	Tibia	OK 141473	2.6	0.9	5.2	15.3	44.2	3.4	This paper
16.	Feryho Tajná Cave	Poz-86754	38800 ± 1000	44396–41801	Mandible	—	6.0	1.0	4.4	15.6	44.3	3.3	This paper
17.	Vavřinecké paleo-ponory Cave	Poz-86794	39500 ± 700	44196–42341	Maxilla	OK 141468	6.5	2.8	11.1	14.2	38.2	3.2	This paper
18.	Feryho Tajná Cave	Poz-65278	41000 ± 1000	45709–42710	Humerus	—	1.6	2.5	7.0	14.3	41.6	3.4	This paper

for European brown bears from the Eemian, Weichselian or early Holocene, making the situation still more unclear, but it is above the scope of this paper to discuss this history in detail.

However, the specific cranial and dental characteristics of several Late Pleistocene brown bears, especially those from periglacial areas, cannot be disputed. There is good evidence from Central and East Europe to north Siberia (e.g., Baryshnikov and Boeskorov 2005; Marciszak et al. 2019 and references therein) that bears from the last glacial period bear a unique combination of features, unknown in recent representatives of the species. The problem is that, with the exception of some Eemian sites (e.g., Taubach, Germany), the record of Late Pleistocene brown bears is rather fragmentary, not allowing the sufficient characterisation of population variability. Therefore, we decided to leave the question of the taxonomic status of Late Pleistocene bears unanswered for the moment and used only informal taxa to describe the morphological characteristics of the studied specimens. We use the term priscus ecomorph for a large form, corresponding to the traditional concept of "*U. a. priscus*" (leaving aside the fact that these phenotypic characteristics do not fit the holotype of *U. a. priscus* itself). The term arctos ecomorph was restricted to the European Late Pleistocene brown bears, phenotypically more or less identical to recent, nominotypical subspecies *U. arctos arctos*. At this time, we were unable to resolve the relationship between these two ecomorphs and their taxonomic status. They can represent just two extremities of the population variability or, e.g., the arctos ecomorph can represent new immigrants from the south or east. Moreover, sometimes the material is so fragmentary that ecomorph determination is not possible. The assignation to the particular ecomorph was made by AM on the basis of a personal study of the material. The present study provides important new information about the temporal distribution of these ecomorphs in the territory of the Czech Republic.

RESULTS

As a result of this research, 18 radiocarbon dates, 16 of which were new, allowed us to specify the Late Pleistocene history of *U. arctos* in the Czech Republic. The dates obtained for brown bears from the Martina Cave (Bohemian Karst) agree with previously published data (Wagner et al. 2016). In most cases, cultural archaeological levels containing brown bear remains are well dated, and ages are consistent, as in the case of Gravettian sites, such as Dolní Věstonice 1 and 2, Pavlov, and Předmostí (Musil 1959, 1967, 1994b, 1997a, 2003a, 2003b, 2018; Wojtal et al. 2012). Some dates obtained for calcined bones, such as those from the Jáchymka Cave (Poz-89020) and Martina Cave (Poz-80462, Poz-86748, Poz-86749), yielded collagen lower than 1%, and the validity of these dates was restricted. All three dates from the Martina Cave cluster are tightly between 40.9–31.2 kyr, called BP, indicating good preservation of the bone, in keeping with a lower collagen amount. As standards, collagen yields above 1% and C/N ratios between 2.9 and 3.6 (DeNiro 1985; Ambrose 1990; van Klinken 1999; Brock et al. 2012) make the dates reliable. However, more recent analysis showed that we should be even stricter in this matter and that collagen with C:N ratios higher than 3.3 and quantity lower than 5% are potentially contaminated and will give dates that are too young (Zazzo et al. 2019). Consequently, some cave dates do not fit well with the proposed age of layers in the analysed material. These dates were probably obtained from remains deposited after the formation of the layer or might have been re-deposited from the younger uppermost horizons. Other dated remains are isolated finds recovered from caves, loess, gravel pits or riverbanks where they occurred in fluvial sediments. In these cases, it should be considered that the material shifted from the place of its original deposition. In addition, it is always important to consider the possibility that humans could have transported some bone parts, such as canines, in the form of precious items over significant distances. Some of the bone collagen samples might have also been contaminated by a young, radiocarbon-enriched source of carbon, probably originating from the soil (Zazzo et al. 2019).

These direct dates showed species' range dynamics during that period. Predicting the response of *U. arctos* to climate allows us to better understand the mechanisms by which species and ecosystems can be affected by climate change (Bellard et al. 2012). The mechanisms of the response of animal populations to climate fluctuations and environmental shifts can also be aided by the study of extinct analogues (Musil 1994a; Hofreiter and Stewart 2009). In these analyses, the transition from the last glaciation to the Holocene (MIS 2) is especially important. This was a time interval when major reorganisation of palaeocommunities and shifts occurred in species distributions as a response to abrupt climate fluctuations (Stewart et al. 2010; Palkoupoulou et al. 2013; Cooper et al. 2015; Nadachowski et al. 2018; Niedziałkowska et al. 2021).

The obtained data showed the continuous presence of *U. arctos* in the Czech Republic in the interval between 46 and 12.6 kyr. Most of the newly obtained dates are concentrated in the range of 45.7–29.3 kyr and covered the second half of MIS 3 (Table 2). The next three dates are especially important because they document the presence of *U. arctos* just before and during the LGM (Last Glacial Maximum, time frames according to Maier et al. 2021). The dates from the sites Pod Hradem (26.5–25.9 kyr), Praha Břevnov (23.4–22.9 kyr) and Praha Bohdalec (22.9–22.3 kyr) imply that this species was present during cold phases of the LGM (Ersmark et al. 2019; Marciszak et al. 2019). The date fits well with the first part of the longest stadial during the LGM (GS-3 and GS-2.1c interval), dated 22.9–20.9 ka (Waelbroeck et al. 2009; Gavashelishvili and Tarkhnishvili 2016). During the coldest (~20.9–19.0 kyr) part of the GS-2.1b interval (20.9–17.5 kyr), the maximum extent of the Scandinavian Ice Sheet had a profound impact on *U. arctos* populations in Europe, including the territory of the Czech Republic. There are indications of gaps in the pattern of dates in certain areas. Available records between 22 and 18 kyr came mostly from southern and southeastern parts of Europe in the alleged refugia (Ersmark et al. 2019). Since 19–18 kyr, European finds of *U. arctos* have considerably increased, and the number of dates was the largest during MIS 2, around the end of GS-2.1b (~17.5 kyr) (Ersmark et al. 2019). The post-LGM time (GS-2.1a interval, 17.5–14.7 kyr) was characterised by intensive climate change processes and a growing number of brown bear dates from the Czech Republic (Table 1). Four radiocarbon dates documented the presence of this species during that time. Finally, the date from Praha-Řeporyje and the Kalvárie Cave (12.8–12.6 kyr) recorded *U. arctos* during the beginning of the LGM, i.e., during abrupt GI-1e (14.7–14.1 kyr) warming (Steffensen et al. 2008).

This was also a period of progressive growth in afforestation and the final disappearance of the steppe tundra in Central Europe. This warming caused a gradual transformation of Europe from semiarid, grassy steppes into boreal forests. Enormous herds of ungulates adapted to live in open grasslands disappeared as the forest took over their grassland habitats. The priscus ecomorph could not scavenge enough food to support its massive body, even if it could supplement its diet with plants. The process of disappearance and its mechanisms are still not resolved. The compact geographical range was split into isolated populations that

Table 2 Occurrence of *Ursus arctos* in the Middle and Late Pleistocene sites of the Czech Republic.

No.	Site	Age in MIS (kyr BP)	Site type	Ecomorph	Sources
1.	Chlum 4	19 or earlier	Cave	Indet.	Wagner and Čermák (2012)
2.	Stránská skála	?	?	Indet.	Musil (1972); this paper
3.	Chlupáčova Cave	5e (130-115)	Cave	Priscus	Mostecký (1961, 1963, 1969)
4.	Kůlna Cave, l. 14	5e (130-115)	Cave	Priscus	Musil (1967, 2010, 2018); Valoch et al. (1970); Valoch (1988)
5.	Vratíkov, Cave no 4	5b	Cave	Indet.	Musil (1967, 2018)
6.	Brno-Bohunice	5b	Open-air	Indet	Musil (1960, 2018)
4.	Kůlna Cave, l. 11	5b	Cave	Priscus	Musil (1967, 1970, 2010); Valoch et al. (1970); Valoch (1988)
4.	Kůlna Cave, l. 9-7	4-3 (70-44)	Cave	Priscus	Musil (1970, 2003a, b, 2018); Valoch et al. (1970); Valoch (1988)
7.	Feryho Tajná Cave	3 (47-42)	Cave	Priscus	Roblíčková et al. (2020)
8.	Vavřinecké paleoponory Cave	3 (45-38)	Cave	Arctos	This paper
9.	Nad Kačákem Cave	3 (40-38)	Cave	Arctos	Diedrich and Žák (2006); this paper
10.	Martina Cave	3 (40-32)	Cave	Arctos	This paper
11.	Šipka Cave	4-2 (27-23)	Cave	Priscus	Musil (1965a, 2018)
12.	Pod Hradem Cave, l. 19-10	3 (38-29)	Cave	Priscus	Musil (1965b, 2018)
13.	Švédův stůl Cave	3 (38-29)	Cave	Priscus	Musil (1962, 1997b, 2018); Matoušek et al. (2005)
14.	Čertova díra Cave, l. 2	3 (38-32)	Cave	Priscus	Musil (1996); Svoboda et al. (2002)
15.	Praha, Svatoprokopská Cave	3 (32-31)	Cave	Arctos	This paper
16.	Výpustek	3-2	Cave	Priscus	Svoboda et al. (2002); Matoušek et al. (2005)
17.	Zkamenělý zámek	3-2	Cave	Indet	Svoboda et al. (2002)
18.	Turold	3-2	Cave	Arctos	Svoboda et al. (2002)

(*Continued*)

Table 2 (*Continued*)

No.	Site	Age in MIS (kyr BP)	Site type	Ecomorph	Sources
19.	Šošůvka Cave	3-2	Cave	Indet	Svoboda et al. (2002); Matoušek et al. (2005)
20.	V Hložku Cave	3-2	Cave	Indet	Svoboda et al. (2002)
21.	Křížova Cave	3-2	Cave	Indet	Svoboda (1999); Svoboda et al. (2002); Matoušek et al. (2005)
22.	Kateřinská Cave	3-2	Cave	Arctos	Geislerová et al. (1986)
23.	Hlavicova Cave	3-2	Cave	Indet	Skutil (1955)
24.	Hadí Cave	3-2	Cave	Arctos	Dvořák (1967)
25.	u Hamru Cave	3-2	Cave	Indet	Šída and Prostředník (2004)
26.	Barová Cave	3	Cave	Priscus, arctos	Roblíčková et al. (2017a, b)
27.	Srnčí Cave	3-2	Cave	Indet	Jarošová (2002); Nývltová-Fišáková (2002)
28.	Sloupské Caves	3-2	Cave	Arctos	Svoboda et al. (2002)
29.	Průchodnice	3-2	Cave	Indet	Svoboda et al. (2002)
30.	Rytířská Cave	3-2	Cave	Indet	Svoboda et al. (2002); Matoušek et al. (2005)
31.	Turská Maštal	LP	Cave	Indet	Kafka (1903); Diedrich and Žák (2006)
32.	Cave near Josefovské údolí	3-2	Cave	Indet	This work
33.	Milovice	3-2 (32-25)	Open-air	Indet	Oliva (2005); Svoboda et al. (2011)
34.	Balcarova skála Cave	3-2 (35-15)	Cave	Indet	Musil (1967)
35.	Pavlov	2 (29-26)	Open-air	Priscus, arctos	Musil (1959, 1967, 1994b, 1997a, 2003a, b, 2018); Wojtal et al. (2012)
36.	Předmostí	2 (29-25)	Open-air	Priscus	Klíma (1990); Musil (2008); Bocherens et al. (2015); Wojtal et al. (2020)
37.	Dolní Věstonice 2	2 (29-24)	Open-air	Priscus, arctos	Musil (2003a, b); Nývltová-Fišáková (2000, 2001, 2002); Wojtal et al. (2018)
38.	Dolní Věstonice 1	2 (29-24)	Open-air	Priscus	Klíma (1995); Oliva (2005)

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Table 2 (*Continued*)

No.	Site	Age in MIS (kyr BP)	Site type	Ecomorph	Sources
39.	Praha-Břevnov	2 (23.5-23)	Open-air	Arctos	This paper
40.	Praha-Bohdalec	2 (22.8-22.2)	Open-air	Priscus	Kafka (1903); this paper
41.	Boršice-Chrástka	2 (17-12)	Open-air	Indet	Nývltová-Fišáková et al. (2006)
4.	Kůlna Cave, l. 6-3	2 (18-11.5)	Cave	Priscus	Musil (1967, 2010, 2018); Valoch et al. (1970); Valoch (1988)
34.	Balcarova Skála Cave	2 (17-14)	Cave	Arctos	Musil (1958a, b, 2002, 2018)
4.	Pekárna Cave	2 (17-12)	Cave	Priscus, arctos	Svoboda et al. (2002); Matoušek et al. (2005)
42.	Sklep	2-1 (17-12)	Cave	Arctos	Svoboda et al. (2002)
43.	Liščí díra Cave	2-1 (17-12)	Cave	Arctos	Dvořák (1967); Svoboda et al. (2002)
44.	Ve Stráni Cave	2-1 (17-12)	Cave	Arctos	Matoušek et al. (2005)
45.	Vinckova Cave	2-1 (17-12)	Cave	Arctos	Svoboda et al. (2002)
46.	Nad Východem	2-1 (17-12)	Cave	Arctos	Svoboda et al. (2002)
47.	Jáchymka Cave	2 (15.6-15)	Cave	Arctos	This paper
24.	Hadí Cave	2 (15.5-15)	Cave	Arctos	This paper
48.	Býčí skála Cave	2-1 (16-10)	Cave	Priscus, arctos	Bayer (1925); Musil (2014)
49.	Kolíbky	1 (14-12.5)	Cave	Priscus	Musil (1967, 2018); Svoboda (1999); Svoboda et al. (2002)
4.	Kůlna Cave, l. 2-1	2 (14-12)	Cave	Arctos	Musil (1958a, b, 2002, 2018); Valoch et al. (1970); Valoch (1988)
50.	Praha, Kalvárie Cave	2-1 (13-12.5)	Cave	Arctos	Kafka (1903); Diedrich and Žák (2006)
51.	Praha, Kotlářka	2-1	Open-air	Arctos	Kafka (1903)

survived across Europe. The decreasing size process took place, and *U. a. priscus* evolved into a more herbivorous form because of environmental changes. Leftovers blend into an abundant nominative form, which is much more herbivorous and omnivorous; they are also well adapted to forest conditions. Survival of the priscus ecomorph until the early part of MIS 1 has been confirmed by numerous finding of the great brown bear with particularly large and broad teeth (Marciszak et al. 2019 and references therein). From the Czech Republic, the late occurrence of the priscus ecomorph was documented by a robust mandible from the Býčí skála Cave, dated to 15.4–14.9 kyr.

DISCUSSION

The earliest possible record of *U. arctos* or at least its form from the arctoid lineage in the Czech Republic originates from the locality Chlum 4S, which is around the Early/Middle Pleistocene boundary in age, but the exact stratigraphical position is unknown at present (Wagner and Čermák 2012; Horáček et al. 2016). New revisions, e.g., Lewis et al. (2010) and Rabeder et al. (2010), showed a higher variability among Middle Pleistocene arctoid bears than previously thought. However, according to Wagner and Čermák (2012), most of these Middle Pleistocene specimens belong to *U. deningeri*. Therefore, a new revision of the members of this lineage seems necessary for a more precise taxonomic determination. Therefore, a new revision of the members of this lineage seems necessary for a more precise taxonomical determination. Even if the presence of the species in the Middle Pleistocene is still not completely resolved, there is no doubt that the majority of the records belong to the Late Pleistocene. From the old collections, Musil (1972: 109) reported two maxillary fragments of *U. arctos* from Stránská Skála, which are in the same collection but differ in fossilisation. However, this material came from old excavations; therefore, its detailed location and exact stratigraphical position are strongly uncertain. Stránská Skála is a complex of large and small cavities and fissures filled with sediments of different ages. For this reason Stránská Skála cannot be regarded as a Middle Pleistocene record of *U. arctos*.

The Eemian (MIS 5e) is the time when true brown bears undoubtedly appeared in Czech territory in a form possibly identical with *Ursus arctos* “*priscus*” sensu lato (but see above regarding the nomenclatural confusion of this subspecies), a characteristic faunal element of European open land assemblages (Kurtén 1968). This large, broad-toothed bear migrated from the East (Figure 1; Musil 1996; Sabol 2001a, b) and appeared first in the late Middle Pleistocene (Kurtén 1959; Baryshnikov 2007; Marciszak et al. 2019; Marciszak and Lipecki 2020). Earlier authors described the Eemian populations as independent subspecies called *Ursus arctos taubachensis* Rode, 1935 (Kurtén 1956, 1959, 1968; Mostecký 1961, 1963, 1969; Musil 1996; Sabol 2001a, b; Wagner 2001). However, its taxonomic position was later revised, and it is now considered to be a synonym for *U. a. priscus* s. l. (Baryshnikov 2007; Marciszak et al. 2019; Marciszak and Lipecki 2020; Stefaniak et al. 2021). The presence of this form during MIS 5e is rarely documented in the Czech territory, e.g., from layers 13–9 of the Kůlna Cave (Musil 2010, 2018), as well as from the Chlupáčova Cave (Mostecký 1961, 1963, 1969; Wagner 2001).

The occurrence of *U. arctos* was documented in 51 Late Pleistocene Czech localities (Figure 2, Table 2). After the Eemian, the number of records considerably increased, with 49 palaeontological records documenting the presence of this species within the Czech territory (Kořenský 1884; Kafka 1903; Skutil 1955; Dvořák 1967; Musil 1962, 1965a, 1967; Mostecký 1963, 1969; Geislerová et al. 1986; Wagner 2001; Nývltová-Fišáková 2002; Matoušek et al.

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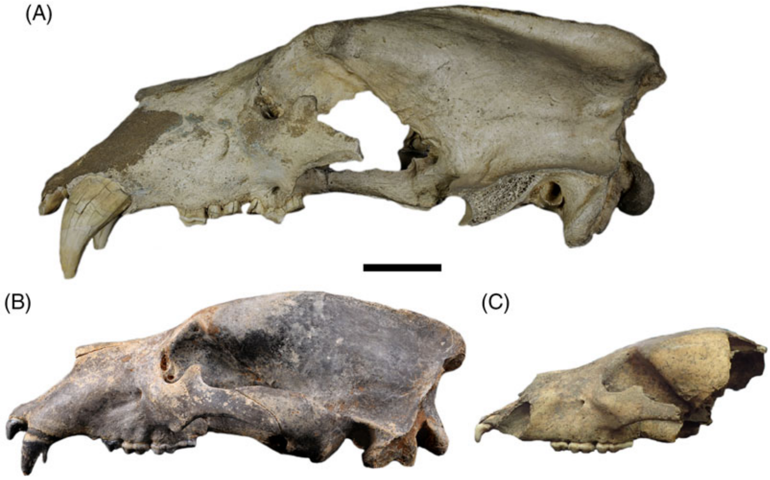

Figure 1 Skulls of the brown bear *Ursus arctos* from the Czech Republic. *Ursus arctos*, priscus ecomorph: A. male from Praha-Bohdalec (NM-R 1916), B. female from Feryho Tajná Cave. *Ursus arctos*, arctos ecomorph: C. female (P 135) from Klučov (P 135; Kudrnáč 1970). Skulls showed in lateral view, scale bar 50 mm. Photos L. Váchová (A), A. Plichta (B), and A. Marciszak (C).

2005; Oliva 2005; Svoboda et al. 2011; Wojtal et al. 2012; Havlová 2014). Among them, there are 10 open-air and 41 cave localities. Plentiful remains have been considered either as a highly divergent form (e.g., Musil 1962, 1964, 1965b, Mostecký 1963), a subspecies of *U. arctos* or as a separate species (Wagner 2001). This mostly depends on which classification system has been used to recognise these forms. For carnivores, several systems have been proposed for different purposes, such as behaviour, ecology or morphological differences. However, the ecotype approach, when a population or a group of populations is associated with a particular set of environmental conditions, is adopted in conservation ecology. Ecotypes classify *U. arctos* according to different life history strategies and ecological conditions. Since the holotype of *U. a. priscus* does not contain the diagnostic characteristics traditionally used for defining this subspecies (Pacher 2007; Marciszak et al. 2019) and so far no formal re-description and/or neotype designation has been made, there is currently no consensus on the taxonomic status of this subspecies. In this paper, we recognise this bear as a distinct ecomorph distinguishing it from the nominotypical *Ursus arctos arctos* Linnaeus, 1758, whose occurrence in Czech territory is mostly related to MIS 1. However, the presence of individuals morphometrically indistinguishable from recent *U. a. arctos* was also sporadically distinguished from the Late Pleistocene (Table 2).

The immense priscus ecomorph roamed on Eurasian Late Pleistocene open grasslands (Baryshnikov and Boeskorov 2005), chasing other carnivores away from their carcasses and gorging themselves on scavenged meat (Marciszak et al. 2019). The significantly higher degree of carnivory in European pre-LGM brown bears, compared with recent *U. arctos*, has been confirmed by stable isotope analyses (Münzel et al. 2011; Bocherens 2015; Bocherens et al. 2015; Ersmark et al. 2019). Some of these authors also suggest that the shift to lower δ^{15}N-values started after the LGM was synchronous with the extinction of speleoid bears. It has been proposed as the cause of this dietary shift, as it opened up a more herbivorous niche for brown bears (Münzel et al. 2011; Bocherens 2015; Mackiewicz

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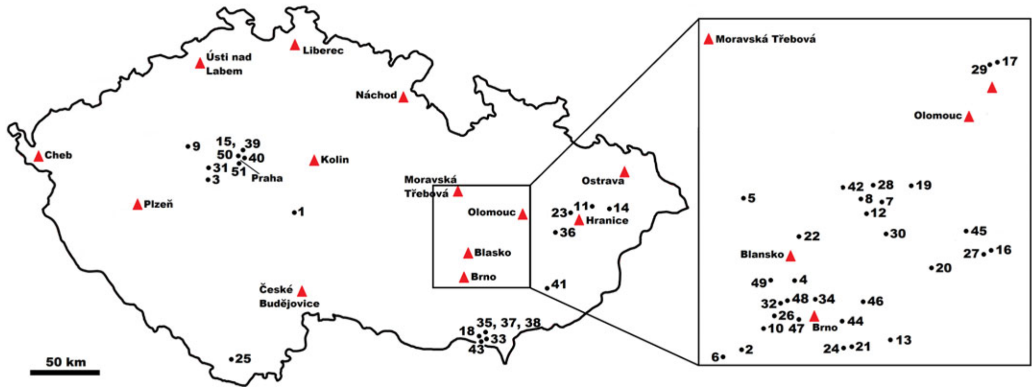

Figure 2 Distribution of the Middle and Late Pleistocene sites with *Ursus arctos* within the Czech Republic. See Table 2 for site numbers.

et al. 2017). However, there is another possible scenario. Higher $\delta^{15}N$ values commonly documented in the Late Pleistocene brown bears from MIS 3 and MIS 2 could have been an adaptation to colder and more barren habitats. Recent *U. arctos* are generally more carnivorous in open landscapes (Bojarska and Selva 2012). Thenius (1956) and Musil (1964) pointed out that *U. a. priscus* occurs in open grasslands. An abrupt warming at 14.7 kyr (onset of GI-1e), a reduction and fragmentation of the priscus-ecomorph range are suggested for a wide area of Europe, except in more oceanic north-western parts, such as the modern Baltic and North Sea coasts and perhaps the central and northern East European Plain. A possible explanation for the longer survival of this large bear is that the steppe-tundra ecosystem in these regions lasted longer. In addition, some areas were much larger because of the presence of a recently inundated huge landmass referred to as Doggerland in the modern North Sea (Coles 2000). During the GI-1 interval (14.7–14.1 kyr), present day Baltic and North Sea coasts, as well as the north-western part of Europe, were still covered by open grassland vegetation suitable for the priscus ecomorph, in contrast to Central Europe, which was already covered by pine forests (Brewer et al. 2017).

CONCLUSIONS

The continuous occurrence of *U. arctos* during the Late Pleistocene (MIS 5e-2) in the territory of the Czech Republic was documented in 51 localities. Among them, 10 were open air sites, while 41 others were cave sites. A total of 18 radiocarbon dates showed the presence of the brown bear between 46 and 12.6 kyr ago during the Late Pleistocene. Most of the dates were concentrated in the range of 45.7–29.3 kyr and covered the second half of MIS 3. Later, its occurrence continued into the Holocene. Three dates documented the presence of *U. arctos* just before and during the LGM. The new dates imply that the species was present during some cold phases of the LGM. During the coldest (~20.9–19.0 kyr) part of the GS-2.1b interval (20.9–17.5 kyr), *U. arctos* was probably absent in the Czech Republic. Similar to other parts of Central Europe, the maximum extent of the Scandinavian Ice Sheet had a profound impact on the Czech brown bears. During the Late Pleistocene, a large, broad-toothed and highly carnivorous priscus ecomorph occurred in the territory of the Czech Republic. It was adapted to live in open grasslands. The post-LGM time (GS-2.1a interval, 17.5–14.7 kyr) was characterised by intense climate changes and a growing

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number of brown bear finds from the Czech Republic. It was also a period of progressive growth in afforestation and the final disappearance of the steppe-tundra biome in Central Europe. It was also the time when the priscus ecomorph evolved into a more herbivorous form because of environmental changes. Leftovers blend into an abundant nominotypical subspecies, which is much more herbivorous and omnivorous, and are also well adapted to forest conditions. A robust mandible from the Býčí Skála Cave, dated at 15.4–14.9 kyr, is so far the latest known occurrence of priscus-ecomorph from the Czech Republic.

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