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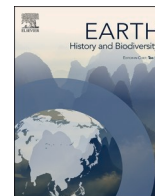
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Distribution history of the cave lion (*Panthera spelaea* (Goldfuss, 1810))

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ABSTRACT

The paper provides an overview of the distribution of the cave lion (*Panthera spelaea*) in Eurasia and North America, spanning the period from the first documented appearance of the species in the fossil record at the end of the Early Pleistocene to its extinction at the end of the Late Pleistocene. A summary of the paleontological materials obtained over the last 50 years, after N.K. Vereshchagin review, is presented. The database utilised in this study encompasses 1044 palaeontological sites and 1506 localities. The hypotheses regarding the migrations (dispersal) of the species, including the migration from Asia to North America, and the timing of extinction in different parts of the range are discussed. The paper presents a synthesis of current research into the distribution of the cave lion, establishing a foundation for further investigation of this distinctive representative of the Pleistocene fauna of the Holarctic.

1. Introduction

The cave lion, *Panthera spelaea* (Goldfuss, 1810), is iconic species occupied the ecological niche of the top predator in Middle and Late Pleistocene ecosystems of Eurasia in the trophic pyramid of mammals. The species was a member of the large carnivore paleoguild, which included such representatives as the sabre-toothed cats, Eurasian "jaguar", tiger, leopards, snow leopards, cheetahs, giant short-faced hyenas, cave hyenas, grey wolf, bears and, with them, members of the genus *Homo*.

The evolution of cave lions *sensu lato*, broadly defined as the temporal succession of chronotaxa and/or the emergence of vicariates in

geographical space in Europe, Asia and North America, as well as their species rank, has long been debated, first in morphological and later in genetic and evolution terms (Schütt and Hemmer, 1978; Turner and Antón, 1980; Kurtén and Anderson, 1980; Kurtén, 1985, 2017; Barycka, 2008; Argant and Brugal, 2017; Baryshnikov and Boeskorov, 2001; Burger et al., 2004; Sotnikova and Nikolskiy, 2006; Barnett et al., 2009, 2016; Mazák, 2010; Marciszak and Stefaniak, 2010; Baryshnikov, 2011; Stuart and Lister, 2011; Sotnikova and Foronova, 2014; Marciszak et al., 2014, 2019; Ersmark et al., 2015; Ghezzi, 2018; Stanton et al., 2020; Hassanin et al., 2021; Villaluenga, 2022; Sablin et al., 2022; Sabol et al., 2022).

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The scientific study of cave lions dates back some 215 years to the "moment" when Georg August Goldfuß described *Felis spelaea* from the famous Zoolithen Cave in 1810 (Bavaria, Germany) (Diedrich, 2008). The remains of cave lions are relatively scarce, which is not surprising given their position in the food chain. As a result, information about cave lion sites and their geographical distribution has been accumulated very gradually, initially mainly within the borders of Western, South and Central Europe (Wolf, 1938). Probably N.K. Vereshchagin made the first detailed description of cave lion localities in the Holarctic (Fig. 1); some 160 years only after the species was first described (Vereshchagin, 1971). In the more than half a century since that publication, the hard work of many researchers has produced a wealth of new material on cave lion finds throughout its vast range, from the British Isles to the province of Alberta (Canada), and from the Arctic Circle to the Middle East. Many sites have been dated, including direct radiocarbon dating of lion remains, but the number of such dates is much smaller than those obtained from the remains of other species associated with the cave lion in the sediments.

In this paper, we consider all cave lions (*P. spelaea*) that inhabited Eurasia and North America during Middle–Late Pleistocene (*P. spelaea fossilis* (von Reichenau, 1906), *P. spelaea intermedia* Argant and Brugal, 2017, *P. spelaea* (Goldfuss, 1810), *P. spelaea vereshchagini* Baryshnikov and Boeskorov, 2001) as representatives of a single phylogenetic lineage (or very closed sister lineages) (Hassanin et al., 2021).

We attempted to bring together in a single database almost all the information currently available on cave lion remains. The vast majority of finds described in numerous publications. However, some finds from the northeast of the species' range are presented here for the first time.

The main aim of our study was described systematically the range of the cave lion from the conventional time of its appearance at the beginning of the Middle Pleistocene (as identified in the palaeontological record) or slightly earlier, to its complete extinction at the end of the Late Pleistocene. The second objective was to try to clarify the likely dispersal routes of cave lions in the Holarctic, based on the available data.

2. Materials and methods

2.1. Regional setting and time "windows"

The cave lion inhabited Eurasia and North America during the Middle and Late Pleistocene (Fig. 2A). This resulted in a large spatial diversity of its habitats due to the variety of local physiographic conditions. However, even greater amplitude of variation in the environment of this chronospecies was associated with global climate changes – periodic long glaciations followed by relatively short interglacial warmings (Fig. 2B).

For convenience in describing the range of the cave lion 13 geographical units – geographical regions – were identified (Fig. 2A). The boundaries of the regions are rather conventional and do not correspond to any intraspecific groupings. At the same time, orography and the presence of potential geographic barriers in the form of large river basins, mountain ranges, etc. were taken into account when identifying these regions.

We used four "time windows" for the Early – Middle Pleistocene (EP, MP-I, MP-II) and Late Pleistocene (LP) (Cohen and Gibbard, 2019) based on the heavy oxygen isotope ($\delta^{18}\text{O}_{\text{‰}}$) curve (Lisiecki and Raymo, 2005) and Marine Isotope Stages (MIS) (Fig. 2B). Most of the palaeontological material comes directly or indirectly from the LP period. In many cases, this has allowed us to refine the description of cave lion distribution by isotopic stage, namely MIS5, MIS4, MIS3, MIS2, and shorter climatic intervals according to the Greenland ice-core records nomenclature (Rasmussen et al., 2014).

2.2. Database

Our database contains descriptions of 1044 geographical palaeontological sites ("points") with cave lion remains (Table 1). Of these, 631 sites (~60 %) were dated using instrumental methods. The number of localities (pits, units, layers, etc.) is 1506.

In the text, we have tried to give site names in European national languages where possible and appropriate, and to follow the spelling of

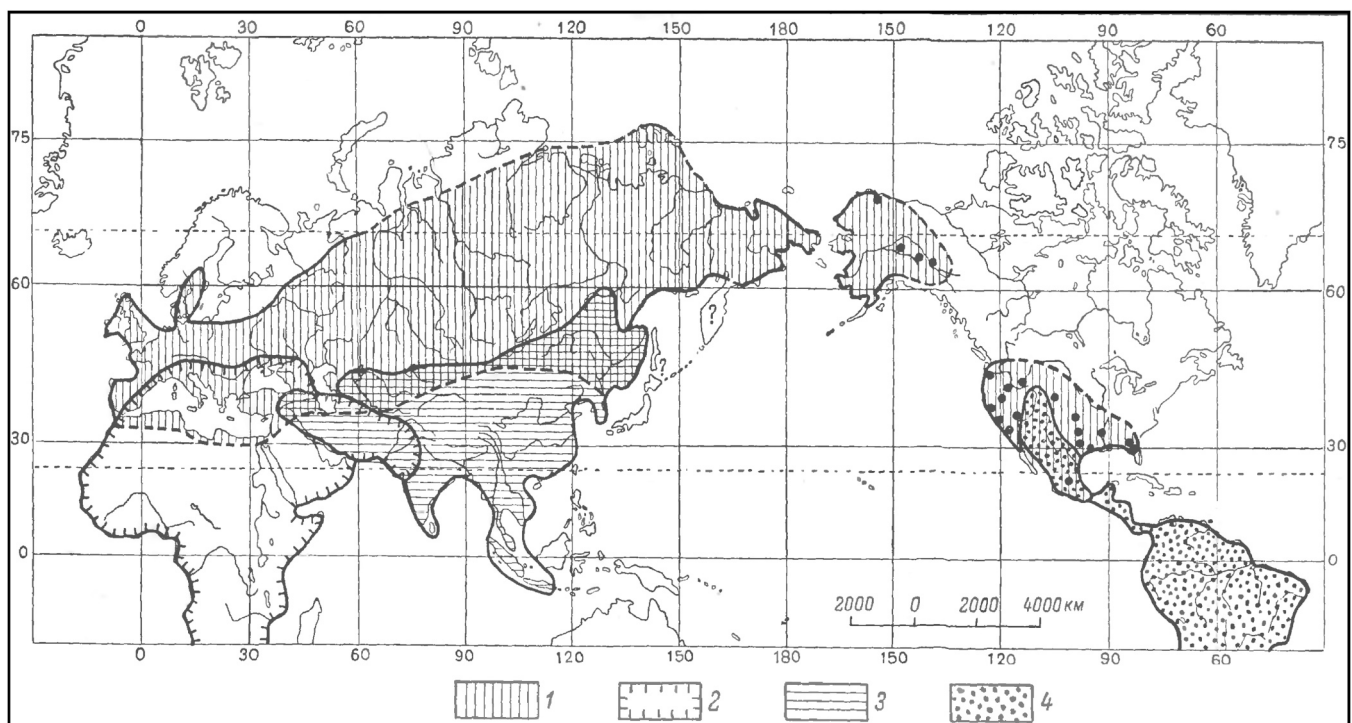


Fig. 1. Ranges of *P. spelaea* and *P. atrox* (1), extant lion (2), tiger (3), and jaguar adopted from ((Vereshchagin, 1971): 161).

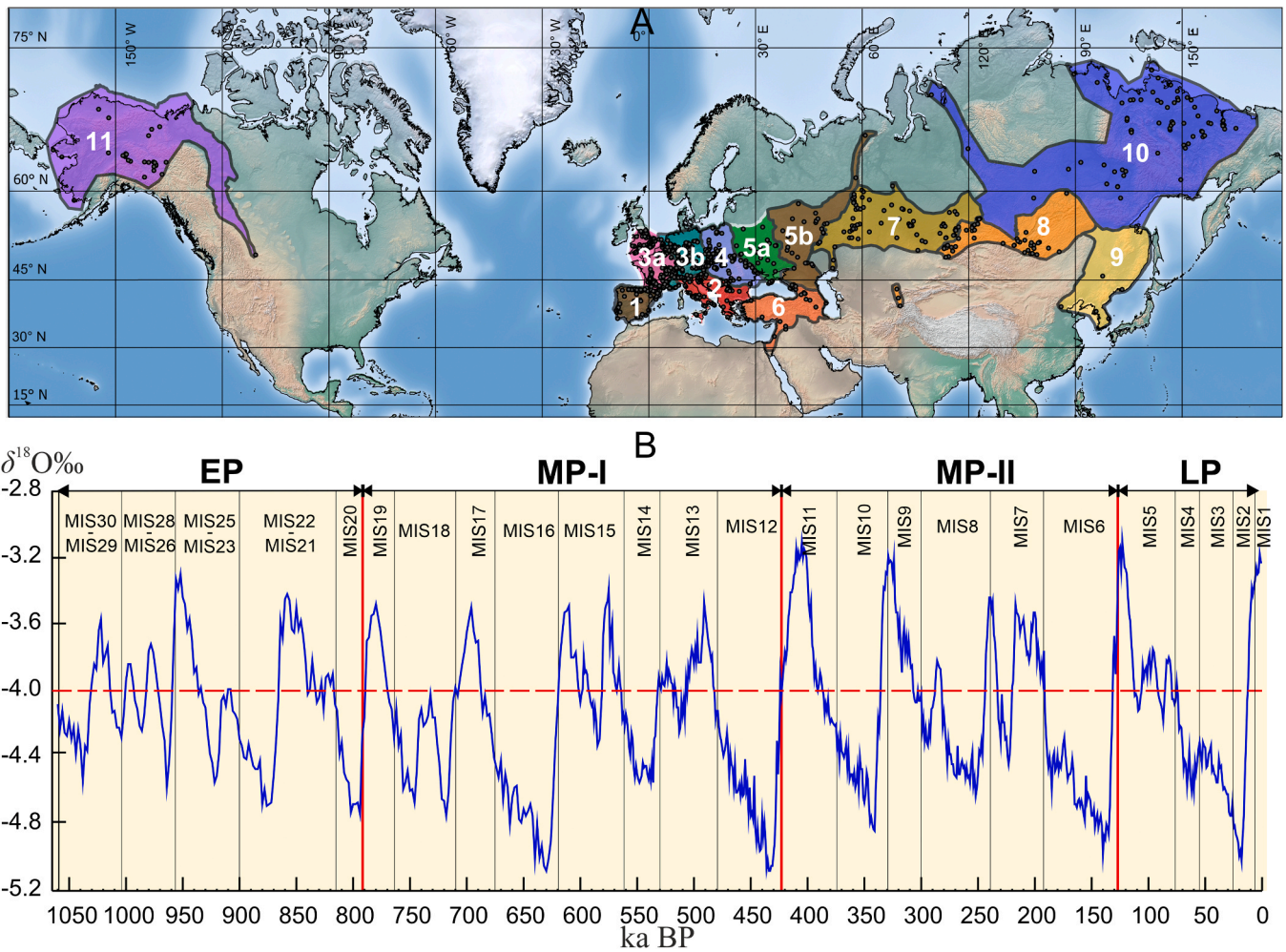


Fig. 2. A – the sites (grey points) with remains of cave lions (*P. spelaea*) and the geographical regions (1–11) used in this study; here and below the raster image "Natural Earth" is used (<https://www.naturalearthdata.com/>). B – "time windows" (EP – MP-II) on the heavy oxygen isotope ($\delta^{18}O$ ‰) curve (Cohen and Gibbard, 2019) and Marine Isotope Stages (MIS).

Table 1
Quantitative description of a database of cave lion remains in Holarctic.

Region (Fig. 2A)	Sites with cave lion remains	Sites dated by instrumental methods	Cave lion remains with direct radiocarbon dates		Localities (pits, units, layers, etc.) of the Middle and Late Pleistocene "periods"			
			finite	infinite	EP ^a	MP-I ^b	MP-II ^c	LP ^d
1	58	44	3	0	0	3	23	64
2	73	43	3	0	2	15	19	79
3a	216	131	13	2	0	16	69	251*
3b	185	95	18	2	1	9	31	258
4	158	90	22	1	1	12	18	187
5a	36	19	3	0	0	1	4	34
5b	31	13	4	0	0	0	9	28
6	21	12	0	0	0	1	8	19
7	67	47	30	8	1	2	17	67
8	82	50	11	0	2	1	11	119
9	5	3	0	0	0	0	3	3
10	79**	52	46	30	3	5	7	70
11	33	32	36	2	0	0	0	33
Total	1044	631	189	45	10	65	219	1212

Comments: a – MIS30–MIS20, b – MIS19–MIS12, c – MIS11–MIS6, d – MIS5–MIS2 (Fig. 2B), * – one more date belongs to the Early Holocene, ** – two other "points" had only regional geographical references.

site names in the cited literature. In other cases, we have used Latin transliteration.

All finite radiocarbon dates have been calibrated in OxCal 4.4. using the IntCal20 calibration curve (Northern Hemisphere) (Ramsey, 2009; Reimer et al., 2020). For stratigraphic units with dates from faunal remains associated with the cave lion and other objects in the database, average dates were given.

The database contains information on 234 radiocarbon dates obtained directly from cave lion remains. Of these, 189 (~81 %) belong to finite dates. 95.4 % confidence intervals are given only for direct data in the database and in the text.

The limited length of the journal publication does not allow the database to be included in the main text. Therefore, the source material (database) for this study is provided in the electronic Supplementary-Material-DataBase in Microsoft Excel format. A complete list of references is also provided in this supplement.

2.3. Data processing

For the regions 1–11, a series of original cartograms were prepared to illustrate the distribution of sites with lion remains within the time intervals EP–MP-II, MIS5, MIS4, MIS3 and MIS2. The generalised boundaries of the ice sheets of the different Pleistocene glaciations were shown on the maps according to (Batchelor et al., 2019).

2.4. Uncertainties in cave lion range reconstruction

We have taken into account some of the almost unresolvable uncertainties associated with palaeo-range reconstruction. Firstly, the uncertainty is due to inaccurate dating of sites or stratigraphic units, including the lack of dates obtained by instrumental methods. In the case of infinite radiocarbon dates, there is also a wide range of interpretation of the results. It should also be borne in mind that there are differences between stratigraphic correlations on zoological and botanical sources. In general, dating uncertainty increases exponentially with the geological age of the site.

The geographical distribution of the palaeontological sites is the second source of uncertainty. For example, the vast majority of cave lion sites in Europe are associated with karst and mountainous areas, i.e. areas where caves are common. At the same time, on the plains, for example in the Paris basin between the Seine and Loire rivers (France), lions may be virtually absent or sporadic. Throughout the cave lion's range, such "white patches" of varying size are quite common. The absence of records within the presumed range does not prove that the animals avoided these areas.

Significant areas of the cave lion's range were periodically covered by ice (Fig. 2A). As the glaciers moved, they destroyed Pleistocene deposits, especially at high latitudes and in mountain regions, and destroyed evidence of animal occupation. For example, there is still no information on the Pleistocene habitation of lions (as well as many other mammals) on the territory of the Middle Siberian Plateau (= Central Siberian Plateau). In this case, in addition to the glacial impact, there was a geological uplift of the area, which resulted in significant erosion of not only quaternary but also earlier sediments.

The third source of uncertainty – misidentification of remains – is present in areas where the ranges of big cats may have overlapped in the past (Fig. 1): cave lions and tigers, cave lions and extant lions.

The source of uncertainty is often the dating of remains based on indirect indicators and "associated" fauna. This is particularly true for the cave lion, as it is mostly found sporadically, even in caves. Dating from associated fauna, especially from river alluvium, is particularly problematic.

Another source of uncertainty that should be mentioned here is due to the development of techniques for measuring the geological age of sediments or biological remains. The results of different physical methods of dating the host sediments may be contradictory. Caution

should also be exercised in interpreting radiocarbon dates obtained in the 70–90 s of the last century, which can sometimes significantly underestimate the age of samples (Jacobi et al., 2009).

Under these conditions, we did not set ourselves the task of reconstructing the boundaries of the cave lion's range, especially in the northern areas. What we have tried to do here is to clarify some of the features of this historical puzzle on the basis of the available data collected by several generations of researchers in different countries.

3. Results

3.1. Region 1 – Iberian Peninsula

In southwest Europe, the oldest (MIS12) evidence for the presence of large cats belonging to the cave lion lineage comes from a group of localities in the Atapuerca area (Spain) (Fig. 3A): Trincherá Galería, Gran Dolina, and Sima de los Huesos (García and Arsuaga, 1998; García et al., 2023). Middle Pleistocene remains dating from MIS11–MIS6 are known from 22 sites. In the MIS6 glacial, the species was reliably recorded in the south of the Iberian Peninsula in the Carigüela Cave (Riquelme Cantal et al., 2024) (Fig. 3A). At the beginning of the LP (MIS5) the range was practically the same as in the Middle Pleistocene. It is possible that the conditions of the first stage of the Last Glacial (MIS4) became unfavourable for cave lions in the south of the Peninsula. In any case, the few finds dating to this period are concentrated in the north, in mountainous areas (Fig. 3C). During the MIS3 stage, lions were first recorded in the southwest of the peninsula (Fig. 3C), and the range reached its historical maximum in this time. We stress that this hypothesis may not be correct and that the increase in the number of sites with lion remains is due to the spread and increase of hominid populations.

The black squares in Fig. 3C here and below mark sites that are most likely Late Pleistocene age, but no more definitive dating exists.

During the MIS2, the range declined, and the vast majority of records come from cave sites in the Cantabrian Mountains. Nevertheless, a possibly isolated group of lions persisted in the southwest of the region (Vale Boi (Casalheira et al., 2013) and Gruta de Salemas (Cardoso, 1996a)) until the end of the Late Glacial Maximum (LGM, (Clark et al., 2009)) (Fig. 3E).

After the LGM, the range continued to decline, and the youngest remains of the cave lion are known from a relatively small area in northern Spain (Fig. 3D).

The latest direct date from Urtiagako Leizea (= Urtiaga) has a 95.4 % interval of 17035–16336 cal years BP (OxA-10121) (Stuart and Lister, 2011), i.e. it falls into the early deglaciation stage (Late Glacial, GS-2.1a).

3.2. Region 2 – Mediterranean

Southern European (Mediterranean) Region includes the areas of the Apennine and Balkan peninsulas with adjacent islands, and Peloponnese. The shelf between them (the bottom of the modern Adriatic Sea) was periodically exposed during periods of sea-level fall in the Pleistocene glacial-interglacial cycle.

The oldest evidence of cave lions in the region comes from MIS27 (Isernia La Pineta) and MIS20 (Slivia) (Fig. 4A) (Sala, 1990; Palombo et al., 2008). It should be noted that the range of dates for layers 3 A of Unit 2 and 3E of Unit 3 from the Isernia La Pineta site where the cave lion remains were found, varies widely and falls within the very wide interval – MIS27 – MIS12. We use the MIS27 stage as a very tentative lower limit for the time of lion presence on the peninsula. It is more likely that the species occupied this territory later, in the first half of the Middle Pleistocene (MIS17–MIS15). Middle Pleistocene remains of cave lions are not abundant in the Apennine Peninsula. A recent report established the presence of the species in the Middle Pleistocene (MIS16) at the Acheulean site of Notarchirico in southern Italy (Iannucci et al., 2024).

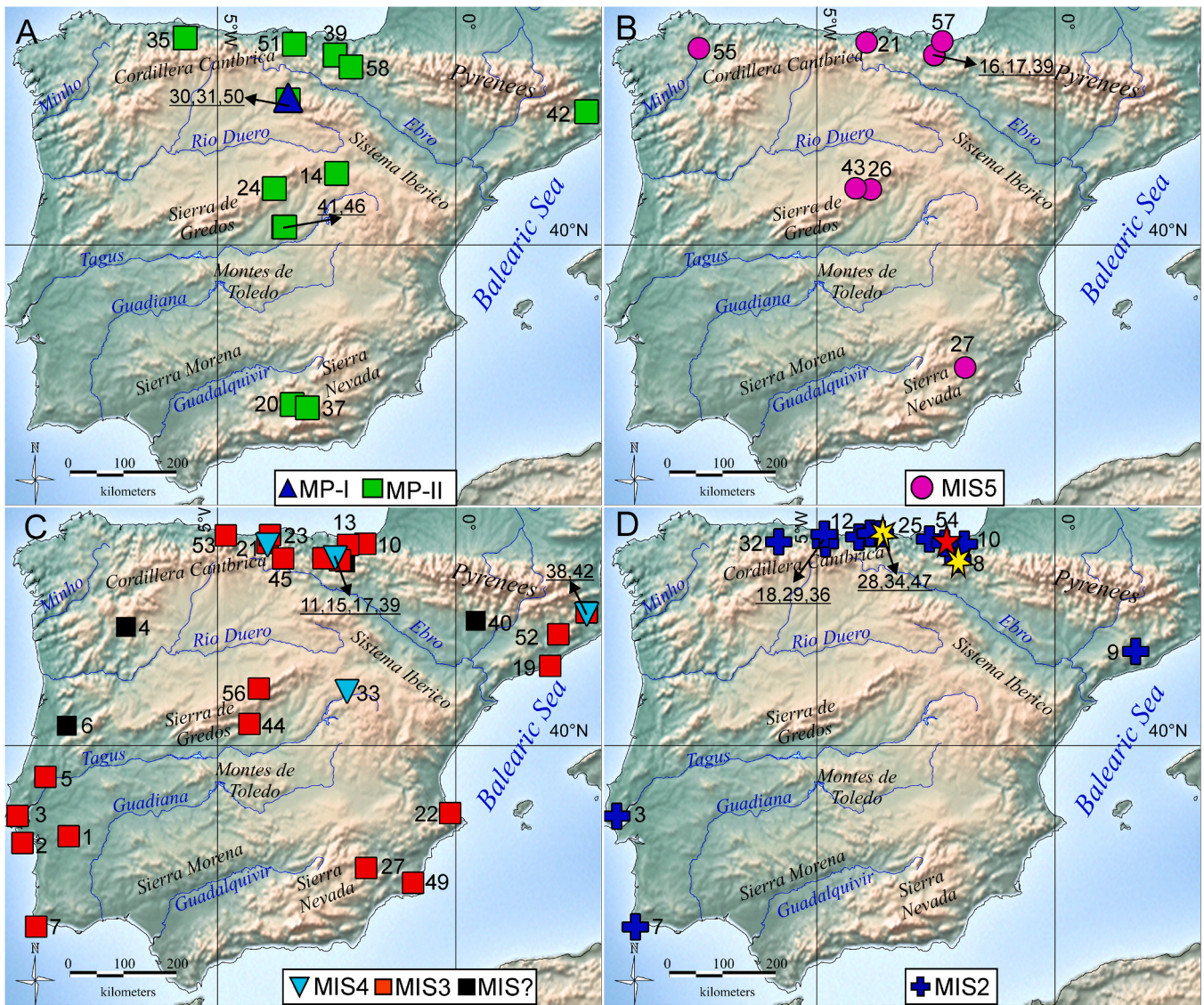


Fig. 3. The sites with cave lion remains in the Region 1 – Iberian Peninsula; the sites with the youngest cave lion remains dated directly (red asterisks) or indirectly (yellow asterisks) are marked: 1 – Escoural, 2 – Figueira Brava Cave, 3 – Gruta de Salemas, 3 – Gruta de Salemas, 3 – Gruta de Salemas, 4 – Lorga de Dine, 5 – Oliveira Cave (Almonda karstic system), 6 – Penacova Gruta, 7 – Vale Boi, 8 – Abautz, 9 – Abric Romaní, 10 – Aitzbitarte III, 11 – Aizkirri, 12 – Altamira, 13 – Amalda Cave, 14 – Ambrona, 15 – Cueva de Arrikrutz, 16 – Artazu VII (Kobate quarry), 17 – Artazu VIII (Kobate quarry), 18 – Balmori La Eria, 19 – Canyars (Terrasses de la Riera dels Canyars), 20 – Carigiuela Cave, 21 – Estrecho Cave, 22 – Cova Foradada, 23 – Cueva d’el Pendo, 24 – Cueva de la Buena Pinta, 25 – Cueva de Santimamiñe, 26 – Cueva del Camino, 27 – Cueva Negra del Castillo del Rio Quipar, 28 – El Juyo, 29 – El Mirón, 30 – Galeria Complex (Trincheria Galeria), 31 – Gran Dolina, 32 – Jou’l Llobu, 33 – La Cueva de Los Casares, 34 – La Garma, 35 – La Parte, 36 – La Riera Cave, 37 – La Solana del Zamborino, 38 – L’Arbreda Cave (Les coves del Reclau), 39 – Lezetxiki, 40 – Los Moros I, 41 – Arenero Manuel Soto, 42 – Mollet Cave, 43 – Pinarillo-1, 44 – Portalon del Tejadilla, 45 – Prado Vargas, 46 – Preresca, 47 – Ruso (cueva del Ruso), 48 – Sima de Azoleta, 49 – Sima de las Palomas del Cabezo Gordo, 50 – Sima de los Huesos, 51 – Sima I, El Polvorín Cave, 52 – Toll Cave, 53 – Torca del Leon, 54 – Urtiagako Leizea, 55 – Valdavara 3, 56 – Zarzamora Cave, 57 – Imanolen Arrobia, 58 – Escombrera de Coscobilo.

In the Middle Pleistocene, lions inhabited the entire region, including the islands of Sicily and the Peloponnese. In the Late Pleistocene range remained was virtually unchanged from the previous period, but, probably, the animals were absent from the extreme south of the Balkans (Pindus Mountains, Peloponnese).

The maximum number of cave lion sites is dated to the MIS3 stage (Fig. 4C). Fossils dated between 39–32 ka BP are known from Italy (La Sassa), Bulgaria (Lakatnik) and Serbia (the Cave above Trajan’s Plaque). We have only three direct dates for cave lion remains in the region within the confidence interval from 39395 to 32330 cal years BP (OxA-11422, OxA-X-2772-34, AA-63887) (Stuart and Lister, 2011; Dimitrijević et al., 2013; Gatta et al., 2022).

M. Massetti and P.P.A. Mazza (Massetti and Mazza, 2013) hypothesised that the cave lion "or an advanced offspring of the species"

survived into the latest Pleistocene or even earliest Holocene particularly south of the 44th parallel and on the Apennine Peninsula as well. We do not rule out this possibility, but for the region there is a significant gap in time between reliable cave lion finds and findings of lion remains dating to the very end of the Pleistocene. Unfortunately, there is still no ancient DNA analysis of these finds to resolve this issue. Therefore, we accept that Late Pleistocene – Early Holocene lion remains from the region (Sigari et al., 2024), as well as from the Iberian Peninsula, are provisory related to the African lion (*P. leo*).

The extinction of the species in the region was gradual, possibly already from the end of MIS3. First, lions disappeared from the Apennines, immediately after the LGM: Palidoro, 19044±135 cal years BP (R-1069) (Belluomini, 1980; Stiner, 1992). The Kozarnika Cave (Danub Basin, Bulgaria, Fig. 4D) is the latest locality with lion remains gave the

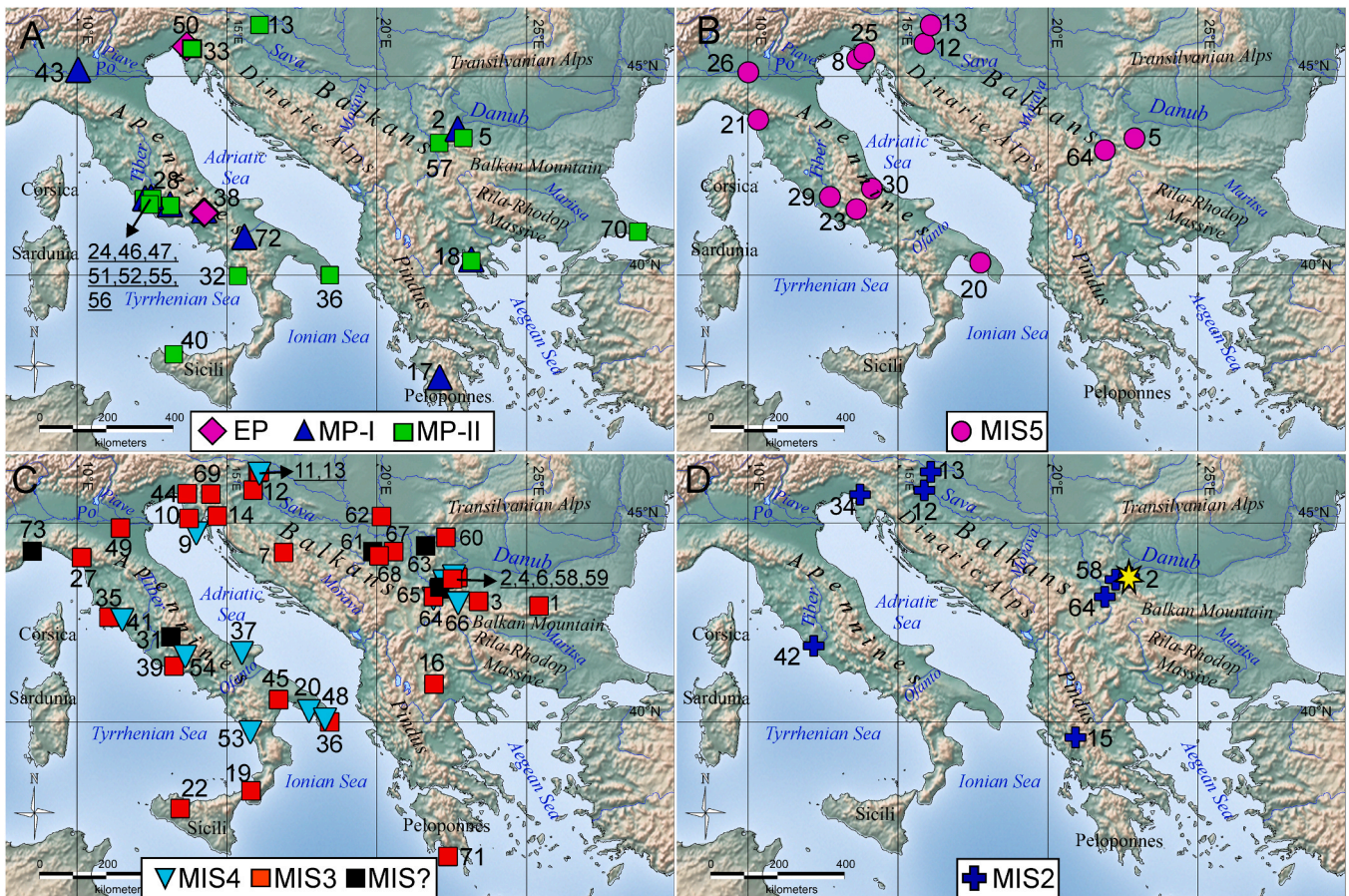


Fig. 4. The sites with cave lion remains in the Region 2 – Mediterranean; the site with the youngest cave lion remains dated indirectly (yellow asterisks) is marked: 1 – Bacho Kiro, 2 –Kozarnika Cave, 3 –Lakatnik, 4 –Mägura Cave, 5 – Mishik Kamik Cave, 6 – Redaka II, 7 –Cerovačke Pećina, 8 – Hijenska Pećina, 9 – Marlera I, 10 –Romualdova Pećina, 11 – Velika Pećina, 12 – Veternica, 13 – Vindija Cave, 14 – Vrtare, 15 – Kastritsa, 16 – Loutrá Aridéas (Loutraki Bear-Cave), 17 – Marathousa-1, 18 – Petralona Cave, 19 – Archi, 20 – Avetrana, 20 –Avetrana, 21 – Buca della Iena, 22 – Cannita Cave, 23 – Carnello, 24 – Castel di Guido (Via Aurelia, 20 km), 25 –Caverna degli Orsi, 26 – Cremona, 27 – Equi Cave, 28 – Fontana Ranuccio, 29 – Fosso del Cupo, 30 – Grotta del Cervo, 32 –Grotta del Poggio, 33 – Grotta dell’Alce (= Grotta Tilde), 34 – Grotta dell’Orso (di Gabrovizza), 35 – Grotta La Fabbrica, 36 – Grotta Romanelli, 37 – Ingarano, 38 – Isernia La Pineta, 39 – La Sassa Cave, 40 – Maccagnone Cave, 41 – Montemerano-Manciano, 42 – Palidoro, 43 – Po River, 44 – Pocala Cave, 46 – Ponte Molle I, 45 – Riparo l’Oscursciuto, 47 – Saccopastore, 48 – San Sidero 3, 49 – Settepolesini di Bondeno, 50 – Slivia, 51 – Torre in Pietra 1, 52 – Torre in Pietra 2, 53 – Torre Talao, 54 – Valle Radice, 55 – Collina Barbattini (Via Aurelia 18.7–19 km), 56 –Vitinia Faunal Unit, 57–59 – Baranica Cave I – II, 60 – Cave above Trajan’s Plaque, 61 – Cave in red rocks at the Medvednik Mountain, 62 – Janda Cavity, 63 – Lazareve Pećine, 64 – Pešturina Pećine, 65 – Prekonoške Pećina, 66 – Propas’ Cave, 67 – Risovača Cave, 68 – Šalitrena Pećina, 69 – Krizna Jama, 70 – Yarimburgaz Cave, 71 – Vlychada Cave, 72 – Notarchirico, 73 – Grotte des Enfants.

average date for the layer OI 13388±106 cal years BP (GifA-98345, GifA-98346) (Fernandez, 2009) that corresponds to the Bölling–Allerød climatic fluctuation (GI-1).

3.3. Region 3a – Western Europe, Atlantic

The region includes the western part of Europe, which is most exposed to the climatic influence of the Atlantic Ocean. During glacial periods, the land area increased at the expense of the continental shelf, including the formation of a land bridge between Britain and the continent. At the same time, ice sheets periodically covered much of Britain. During the interglacial periods, as global sea level rose, the land bridge disappeared and animal populations became isolated on the island.

The oldest remains of members of the cave lion lineage in the region date very roughly to the ~MIS21–MIS17 interval (EP–MP-I time windows). Interestingly, they all come from southeast Great Britain: West Runton Forest Bed/Freshwater Bed and Pakefield (Kessingland) localities (Stuart and Lister, 2001; Gibbard et al., 2010; Lewis et al., 2010; Preece and Parfitt, 2012). If these dates are correct, then lions should have reached this territory no later than ~900 ka BP.

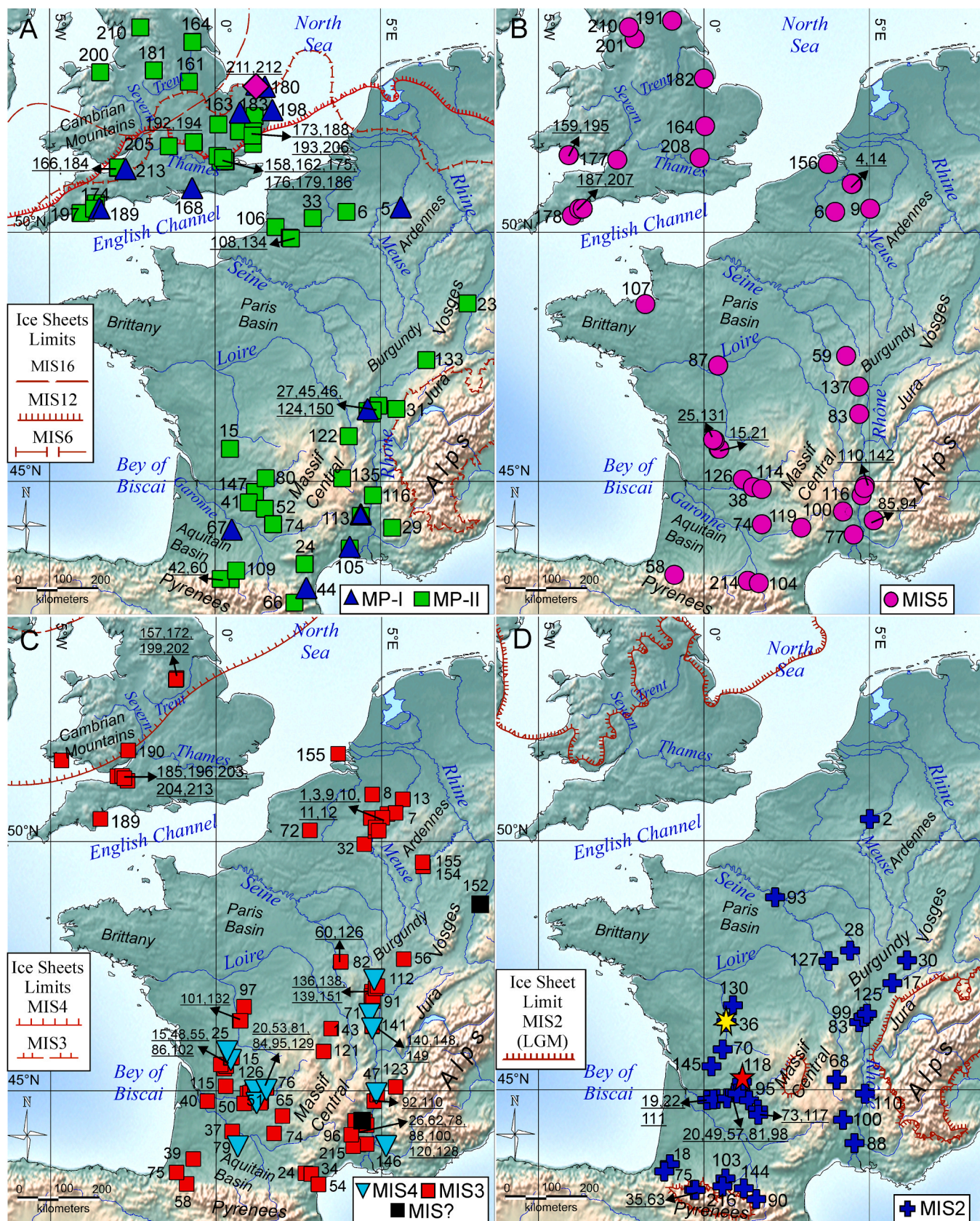
In continental Europe, the earliest evidence of cave lions in the region comes from localities dating back to ~MIS15–MIS14: Château Breccia (Northern section, breccia 3 and 2), Belle-Roche locality (Moigne et al., 2004; Argant et al., 2007), and possibly Caune de l’Arago (middle complex, Ensemble I).

Sites with lion remains in the Late Middle Pleistocene are more numerous, but not evenly distributed across the region. Fig. 5A shows the geographical "gap" between "British" and "continental" site groups in the Middle Pleistocene (MP-I time window). We find it difficult to interpret this unevenness, other than to note that it persists to some extent into the Late Pleistocene (Fig. 5B–5D).

In the Late Pleistocene, the range of cave lions in the region retains the structure developed at the end of the Middle Pleistocene. The only exception to this is sites dating to MIS4, which were only found in the south of the region (Fig. 5C). Also, note the relative decline in the number of sites in Great Britain since MIS3.

Finds of lions in MIS2 are less numerous, but the range size does not appear to have changed much before the extinction process began at the end of this isotopic stage, except Britain.

In Britain, dated remains of the species in age 48288–31788 cal years BP were obtained from the Kent’s Cavern and Pin Hole Cave (OxA-1806,



(caption on next page)

Fig. 5. The sites with cave lion remains in the Region 3a – Atlantic Western Europe; the sites with the youngest cave lion remains dated directly (red asterisk) or indirectly (yellow asterisk) are marked: 1 – Caverne Marie-Jeanne, 2 – Goyet, 3 – Grotte du Docteur, 4 – Hofstade, 5 – La grotte de la Belle-Roche, 6 – Mesvin IV, 7 – Ramioul Cave, 8 – Rotselaar, 9 – Scladina Cave, 10 – Spy Cave, 10 – Spy Cave, 11 – Trou du Sureau (Grottes de Montaigne), 12 – Trou Magrite, 13 – Veldwezelt-Hezerwater, 14 – Zemst (Bos van Aa), 15 – Abri Bourgeois-Delaunay - Abri Suard (la Chaise), 16 – Abri de Cro-Magnon, 17 – Abri des Cabônes (Ranchot), 18 – Abri Duruthy, 19 – Abri Morin, 20 – Abri Pataud, 21 – Abri Pintaud-Gaudry-Paignon, 22 – Abri Vidon, 23 – Achenheim, 24 – Aldène, 25 – Artenac, 26 – Aven de l'Arquet, 27 – Azé Cave 1, 28 – Bâlot (Grotte de la Roche aux Chats), 29 – Bau de L'Aubesier, 30 – Baume Cave, 31 – Baume de Gigny, 32 – Bayol Cave, 33 – Biache-Saint-Vaast, 33 – Biache-Saint-Vaast, 34 – Bize Cave, 35 – Bois du Cantet, 36 – Bois Ragot, 37 – Bourdette, 38 – Bramefond Cave (Souillac Cave), 39 – Grotte des Hyènes, 39 – Grotte des Hyènes, 40 – Camiac, 41 – Camps-de-Peyre, 42 – Cap de la Bielle Cave, 43 – Castelmerle (Abri Castanet), 44 – Caune de l'Arago, 45 – Château Breccia (Northern Section), 46 – Château Breccia (Southern Section), 47 – Châteaubourg, 48 – Chauverie, 49 – Combarelles, 50 – Combe Capelle Bas, 51 – Combe Grenal, 52 – Coudoulous I, 53 – Coustal (carrière), 54 – Crouzade, 55 – Fontéchevade, 56 – Abri Cuvier, 57 – Gare de Couze, 58 – Gatzarria Cave, 59 – Brèche de Genay, 60 – Gerde (La Carrière Cave), 61 – Grande Grotte, 62 – Grotte Chauvet, 63 – Grotte d'Aurensan, 64 – Grotte de Combe Obscure, 65 – Grotte de Foissac, 66 – Grotte de la Carrière, 67 – Grotte de la Nauterie I, 68 – Cottier Cave, 69 – Figuier Cave, 70 – Grotte du Gros Roc, 71 – Grottes de Curtil-sous-Burnand, 72 – Hénin-sur-Cojeul, 73 – Igue de la Bergerie, 74 – Igue des Rameaux, 75 – Isturitz Cave, 76 – Jarens, 77 – La Balauzière Cave, 78 – La Baume Longue, 79 – La Calmette Cave, 80 – l'Aven II Abîmes de La Fage, 81 – La Ferrassie, 82 – La Garenne (grotte 4), 83 – La Grotte des Furtins, 84 – La Madeleine, 85 – La Masque, 86 – La Quina, 87 – La Roche Cotard, 87 – La Roche Cotard, 88 – La Salpêtrière, 89 – La Soute Cave, 90 – La Vache, 91 – La Verpillère 1 (Germolles Cave), 92 – La Voulte (Taupenas Cave), 93 – Le Closeau, 94 – Le Grand Abri aux Pucés, 95 – Le Plage, 96 – L'Ermitage Cave near Alès, 97 – Les Cottés, 98 – Les Eyzies (Richard Cave), 99 – Les Mâcherons, 100 – Abri-des-Pêcheurs, 101 – Les Plumettes, 102 – Les Rois, 103 – Lespugue (Scilles Cave), 104 – L'Herm Cave, 105 – Lunel-Viel, grotte 1 (Mas des Caves), 106 – Menchecourt, 107 – Mont-Dol, 108 – Montières-les-Amiens, 109 – Montmaurin (Coupe Gorge Cave), 110 – La Baume Moula-Guercy, 111 – Moulin-Neuf, 112 – Neuvon Cave, 113 – Orgnac 3, 114 – Padirac (Gouffre), 115 – Pair-non-Pair, 116 – Payre, 117 – Pech-Merle, 118 – Peyrat Cave, 119 – Peyre I, II, 120 – Pondres Cave, 121 – Pont-du-Château (Puy-de-Dôme), 122 – Prajoux-Q, 123 – Presles Cave (Grotto de Prélétang), 124, 125 – Prény-Lacrost 1, 2, 126 – Regourdou Cave, 127 – Grotte du Renne at Arcy-sur-Cure (Renne Cave), 128 – Réseau Salomé, 129 – Roc de Combe, 130 – Roc-aux-Sorciers (Taillebourg Cave), 131 – Grotte de Rochelot, 132 – Rochers-de-Villeneuve, 133 – Romain-la-Roche, 134 – Saint-Acheul, 135 – Sainte-Anne I, 136 – Saint-Romain (Grenier Cave), 137 – Santenay (Pointe du Bois), 138 – Santenay (Pointe Saint-Jean), 139 – Savigny (Combe d'Orange 1), 140, 141 – Solutré 1, 3 (La Roche de Solutré), 142 – Soyons-Réseau (Ursus Cave), 143 – Theillat, 144 – Trois-Frères Cave (engraving of the P. spelaea), 145 – Trou du Cluzeau, 146 – Vallescure, 147 – Grotte Vaufray, XIV, 148 – Vergisson I (Tasnieres Cave), 149 – Vergisson II, 150 – Verzé Cave, 151 – Villers-la-Faye, 152 – Am Hasenkopf, Lichtenau, 153 – Altwies, 154 – Oetrange, Plateau Haed, 155 – North Sea, 156 – Zeeland, Westerschelde, 157 – Ash Tree Cave, 158 – Aveley, Sandy Lane Quarry and A13 sites, Purfleet road, 159 – Bacon Hole, 160 – Bacon, Forest Bed Formation, 161 – Balderton Sand and Gravel, 162 – Barnfield pit (Swanscombe skull site), 163 – East Farm Barnham, Suffolk, 164 – Barrington Chalk Pit, 165 – Bielsbeck Farm, 166 – Bleadon Cave, 167 – Bielsbeck, 168 – Amey's Eartham Pit, Boxgrove, 169 – Brunton, 170 – Cathole Cave, 171 – Cave 8, Uphill quarry, 172 – Church Hole Cave, 173 – Clacton-on-Sea, 174 – Cow Cave, 175 – Crayford, 176 – Dierden's Pit, 177 – Durdham Down Fissure, 178 – Eastern Torrs Quarry Caves, 179 – Ebsfleet, Southfleet Road, 180 – Grantchester, 181 – Hindlow Quarry, 182 – Hoe Grange Quarry Cave, 183 – Hoxne, 184 – Hutton Bone Caves, 185 – Hyaena Den, 186 – Ingress Vale, 187 – Joint Mitnor Cave, 188 – Jordan's Pit, 189 – Kent's Cavern, 190 – King Arthur's Cave, 191 – Kirkdale Cave, 192 – College Farm, Lower Channel, 193 – Maidenhall and Stoke Tunnel, 194 – Marsworth, 195 – Minchin Hole, 196 – Ogof-yr-Ichen, 197 – Oreston caves, 198 – Pakefield/Kessingland, 199 – Pin Hole Cave (Creswell Crags), 200 – Pontnewydd Cave, 201 – Raygill Fissure, 202 – Robin Hood's Cave, 203 – Sandford Hill, 204 – Soldier's Hole, 205 – Stanton Harcourt, 206 – Stutton, 207 – Tornewton Cave, 209 – Uphall pit, Ilford, 210 – Victoria Cave, 211 – West Runton Forest Bed, 213 – Westbury-Sub-Mendip, Broadmead Quarry, 214 – Grotte de Malarnaud, 215 – Grotte de la Verrerie de Macassargues, 216 – Grotte de l'Éléphant.

OxA-13456, OxA-14285, OxA-19092) (Stuart and Lister, 2011; Jacobi and Higham, 2011; Higham et al., 2006, 2011). This means that the lion could have survived there until the end of the MIS3 stage (Denekamp interstadial). The youngest dates – 26700 cal years BP (Birm-340) and 28770 cal years BP (OxA-5805) were obtained on associated fauna (*Coelodonta antiquitatis*, *Rangifer tarandus*) from the Ogof-yr-Ichen and Hyaena Den sites respectively (Van Nederveelde et al., 1973; Tratman et al., 1971). However, these dates are most likely "rejuvenated", considering the years of their publications. Following A.J. Stuart and A. M. Lister (Stuart and Lister, 2011), we suggest that the cave lion went extinct in Britain no later than the end of MIS3 and did not recolonise the island in MIS2, after the LGM.

In the east and south of the region, extinction occurred much later (Fig. 5D), during MIS2. At the beginning of the LGM, a "grouping" that lived west of the Ardennes, in the Meuse basin, disappeared. A date for cave lion remains was obtained from the Goyet Cave with a confidence interval of 29165–28117 cal years BP (KIA-22276) (Bocherens et al., 2011). The territory was most likely not recolonised by the lion after the LGM.

The youngest lion remains from the region are from the Peyrat Cave (France) dated to the Younger Dryas cooling (GS-1), between 12733–12472 cal years BP (SacA-38311) (Fosse et al., 2017). At the Bois Ragot, layers 5 and 6 with cave lion remains dated of 11598±244 cal years BP (Gif-2537) and 11874±329 cal years BP (Gif-3579), respectively (Griggo, 1996). Therefore, we cannot exclude the possibility that the species was present in the region until the beginning of the Holocene (Early Preboreal).

3.4. Region 3b – Western Europe, eastern part

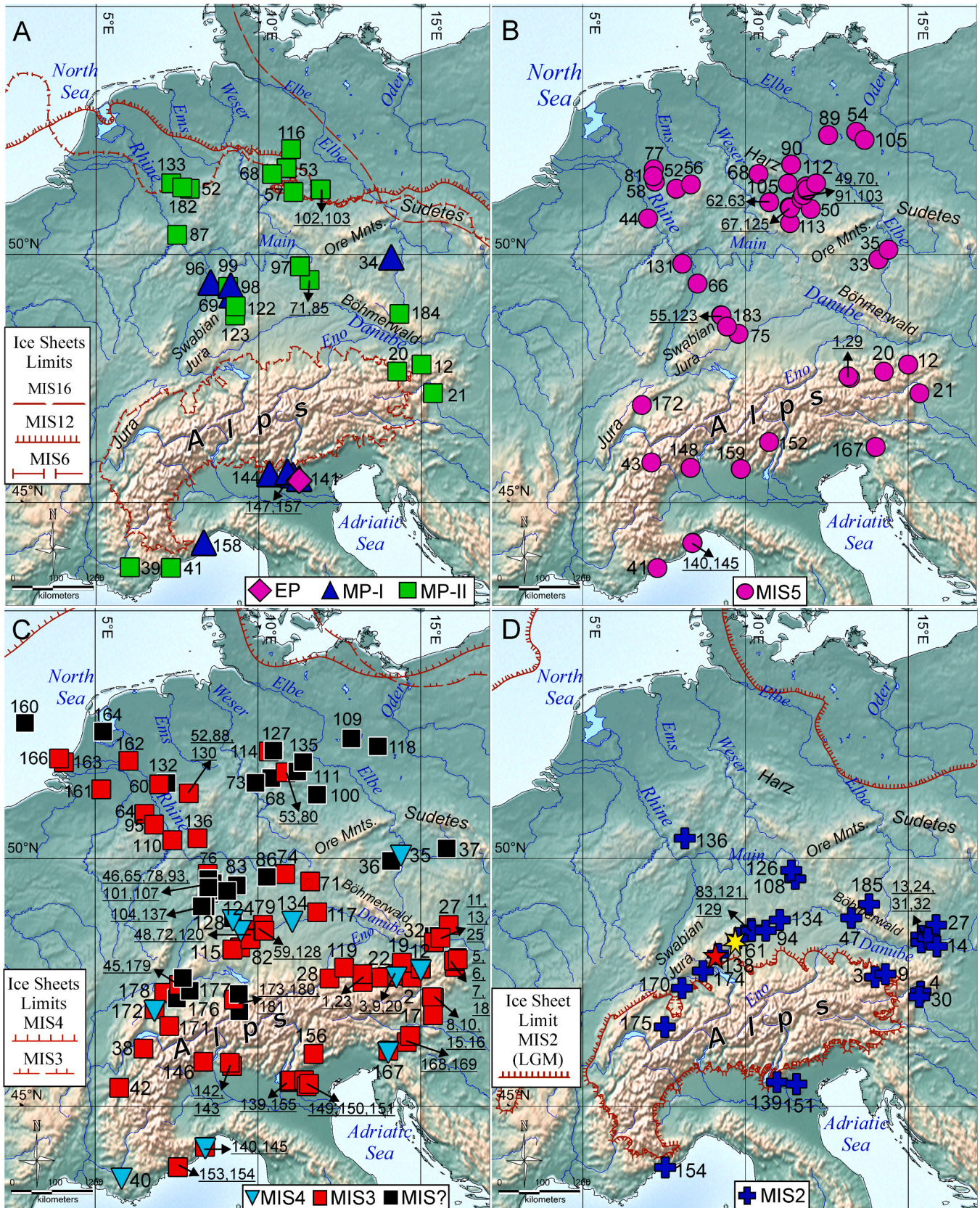
The eastern part of West Europe (Region 3b) includes the Alpine region and the basins of rivers such as the Rhine, Weser, Elbe, and upper

and middle Danube. Its boundary with Region 3a is very tentative, and from Region 4 that locates to the east, it follows the interfluvium of the Oder and Elbe Rivers.

The northern part of the region was regularly covered by ice sheets during the Middle and Late Pleistocene, but the maximum was during the Elster Glaciation (MIS12) (Fig. 6). Mountain glaciation in the Alps was probably continuous over the period considered. Glaciers maximally covered the Alps during the Saale Glaciation (MIS6), and the area covered by ice was slightly smaller during the Würm/Weichselian Glaciation in the Late Pleistocene (Glückert, 2017). An active degradation of the alpine glaciers had already begun by around 23000 cal years BP (Monegato et al., 2017).

Cave lion remains are known from the Breccia di Soave site (Italy) in the extreme south of the region (Fig. 6A). Based on the mammalian fauna composition, their age corresponds to the ~MIS28 stage (EP) (Bona and Sardella, 2012). Also at ~MIS19 stage in the south of the region, the species was found in the Serbaro di Romagnano (Kotsakis and Palombo, 1979). Later, between ~MIS18–MIS12 (MP-I), the range of the cave lion extends northwards to about 49°55'N (Koněprusy – Zlatý kůň, Czech Republic). At the end of the Middle Pleistocene, the northernmost localities are known from Germany at latitudes ~50°–52°N. In the Last Interglacial only a few sites north of 52°N are known (Berlin-Kreuzberg, Kleinbesten and Niederlehme). The northernmost find of lion remains in the North Sea (Brown Ridge, Fig. 6C) probably belongs to the late cold interval of MIS5, but not to the Eemian Interglacial. We cautiously suggest that Late Pleistocene localities north of ~52°N, which are not associated with any isotopic stage (Phoeben, Senzig, Marker Wadden) (Fig. 6 C), may belong to MIS5.

During the MIS4 cooling period (Transitional and First Glacial Maximum SPECMAP climate Phases), the northern limit of distribution of sites with cave lion remains dropped slightly southwards to about 50°N (Praha-Podbaba, Vltava basin) (Fig. 6C). Then, at the beginning of



(caption on next page)

Fig. 6. The sites with cave lion remains in the Region 3b – Western Europe (eastern part); the sites with the youngest cave lion remains dated directly (red asterisk) or indirectly (yellow asterisk) are marked: 1 – Windischkopf-Bärenhöhle, 2 – Bärenhöhle im Hartlesgraben bei Hieflau, 3 – Brettsteinbärenhöhle, 3 – Brettsteinbärenhöhle, 4 – Drachenhöhle bei Mixnitz, 5 – Einhornhöhle bei Dreistetten, 6 – Felsenkeller, 7 – Flutzer Tropfsteinhöhle, 8 – Frauenhöhle, 9 – Gamssulzenhöhle, 10 – Großen Badlhöhle, 11 – Gudenushöhle, 12 – Herdengelhöhle, 13 – Krems-Hundssteig, 14 – Langmannersdorf, 15 – Leopoldinengrotte, 16 – Lurgrotte Peggau, Große Peggauerwandhöhle, 17 – Mehlwurmhöhle, 18 – Merkenstein-Höhle, 19 – Nixloch Cave, 20 – Ramesch-Knochenhöhle, 21 – Repolusthöhle, 22 – Salzföhle, 23 – Schlenkendurchgangshöhle, 24 – Schusterlucke Cave, 25 – Senftenberg, 26 – Tennengebirge, 27 – Teufelslucke, 28 – Tischofer-höhle (Schoferhöhle), 29 – Torrener Bärenhöhle, 30 – Tropfsteinhöhle am Kugelstein, 31 – Willendorf I, 32 – Willendorf II, 33 – Chlupáčova sluj, 34 – Koněprusy – Zlatý kůň, C 718, 35 – Praha-Podbaba, 36 – Berounka, 37 – Svobodné Dvory, 38 – Baré d'Onnion Cave, 39 – Baume Bonne, 40 – Rigabe Cave, 41 – Lazaret, 42 – Les Eugles Cave, 43 – Mars, 44 – Alfter, 45 – Allmendweg, 46 – Altusheim, 47 – Aschenstein, 48 – Aufhausener cave, 49 – Bad Kösen, 50 – Bad Köstritz, 51 – Bad Lauchstädt, 52 – Balver Höhle, 53 – Baumanshöhle, Rübeland, 54 – Berlin-Kreuzberg, 55 – Biedermann travertine, 56 – Bilsteinhöhle, Tropfstein Cave – part of the Bilstein Caves, 57 – Bilzingsleben II, 58 – Bochum, 59 – Bocksteinhöhle, Törle, 60 – Bottrop, 61 – Brillenhöhle, 62 – Burgtonna I, 63 – Burgtonna I-III, 64 – Coenen brick quarry, Ziegeleigrube Coenen, 65 – Deutschof, Speyer, 66 – Edingen, Brühl 1, Edinger Ried, 67 – Ehringsdorf, Weimar, 68 – Einhornhöhle, Unicorn Cave, 69 – Frankenbach, 70 – Freiburg (Unstrut), 71 – Zoolithenhöhle, 72 – Geißenklösterle-Höhle, 73 – Göttingen, 74 – Gremsdorf, 75 – Große Grotte, 76 – Groß-Rohrheim, 77 – Haltern am See, 78 – Heddesheim, 79 – Heidenschmiede rockshelter, 80 – Hermannshöhle, 81 – Hertzen-Stuckenbusch, 82 – Hohle Fels, 83 – Hohlenstein-Stadel, 84 – Hohler Stein Cave, 85 – Hunas, 86 – Huttenheimer Kammer, 87 – Kärlich, 88 – Kepplerhöhle, 89 – Kleinbesten, 90 – Königsau, 91 – Körbisdorf, 92 – Kreuzwiese, 93 – Lampertheim, 94 – Langmahdhalde, 95 – Lommersum, 96 – Grafenrain sandpit, Mauer, 97 – Moggaster Höhle, 98 – Mörtelstein-Obrighheim, 99 – Mosbach 2, 100 – Mücheln, 101 – Neuhofer Altrhein, 102 – Neumark-Nord 1, 103 – Neumark-Nord 2/2, 104 – Neureutm, 105 – Niederlehme, 106 – Oberröblingen, 107 – Otterstadt, 108 – Petershöhle bei Hartenstein, 109 – Phoben, 110 – Plaidter Hummerich, 111 – Quedlinburg, Sevecken, Berge, 112 – Rabutz, 113 – Saalfeld, Fuchsluken, 114 – Salzgitter-Lebenstedt, 115 – Schafstall I and II Rock Shelters, 116 – Schöningen, 116 – Schöningen, 117 – Schulerloch, 118 – Senzig, 119 – Siegsdorf, 120 – Sirgenstein Cave, 121 – Spitzbubenhöhle, 122 – Steinheim an der Murr, 123 – Stuttgart-Untertürkheim, 123 – Stuttgart-Untertürkheim, 124 – Sybillenhöhle, 125 – Taubach, 126 – Teufelsbrücke, Devil's Bridge Cave, 127 – Thiede, 128 – Villa Sekkendorf, 129 – Vogelherd Cave, 130 – Volkringhauser Höhle, 131 – Wallertheim, 132 – Wanne, 134 – Weinberghöhlen bei Mauern, 135 – Westeregeln, 136 – Wildscheuer Cave, 137 – Wörth am Rhein, 138 – Zigeunerfels, 139 – Abri Fumane, 140 – Arma delle Manie, 141 – Brece di Soave, 142 – Buco del Piombo, 143 – Buco dell'Orso Cave, 144 – Cava Zanola, 145 – Caverna delle Fate, 146 – Caverna delle Streghe, 147 – Cerè Cave, Tana dell'Orso, La Tanasela, 148 – Ciota Ciara Cave, 149 – Covoli di Velo Cave, 150 – Grotta di Paina, Azzura di Paina, 151 – Grotta del Broion (Sala Grande), Buso doppio del Broion, 152 – Grotte Conturines, 153 – La grotte du Prince, 154 – Riparo Mochi, 155 – Riparo Tagliente, Abri Tagliente, Stallavena di Grezzana, 156 – San Donà di Lamon, Bus de la Bela, 157 – Serbaro di Romagnano, 158 – Valdemino Cave, 159 – Zandobbio, 160 – Channal, 161 – De Groote Wielen, 162 – Latham, 163 – Maasvlakte, 164 – Marker Wadden, 165 – near the Brown Ridge/North Sea, 166 – Eurogeul, 167 – Divje babe I, 168 – Mokriška Jama, Medvedja Jama, 169 – Potočka Zijalka, 170 – Aarau, 171 – Bärenloch, Charmey, 172 – Cotencher, 173 – Drachenloch II, 174 – Kesslerloch Cave, 175 – Kilchlihöhle, Chilchlihöhle, 176 – Lüsslingen, 177 – Olten-Hammer, 178 – Saint Brais I, II, 179 – Schalbergfelsen höhle, 180 – Wildenmannsloch, 181 – Wildkirchli, 182 – Dechenhöhle, 183 – Erkenbrechtsweiler, 184 – U Hamru Cave, 185 – Sudslavická Cave.

the MIS3 stage (Stable Warm Phase), there was a recovery of the cave lion range (Fig. 6C).

The northernmost record of a cave lion from the early LGM (MIS2) known from the Wildscheuer Cave (Germany), located at ~50°25'N. In general, the northern limit of the distribution of sites with species remains dropped significantly southwards at this time (Fig. 6D).

Based on the available data, it can be assumed that the extinction of the cave lion occurred slightly earlier in this part of Europe than in the west, in region 3a. In addition, by the end of MIS3 and the beginning of MIS2, animals disappeared from the north and north-west of the region. During the LGM and Late Glacial time, the lion survived mainly north of the Alps (Fig. 6D).

According to direct and indirect dating, the last group of cave lions in the region persisted south of the Swabian Jura until the end of the deglaciation and the Bölling-Allerød warming (GI-1) (Fig. 6D). A lion remains from the Zigeunerfels dated between 14846–14168 cal years BP (OxA-17268) (Stuart and Lister, 2011), which falls within the Bölling warming. There is also a slightly earlier indirect date of 14817±178 cal years BP (OxA-23414) from the Brillenhöhle (layer V) obtained on a human bone (Orschiedt, 2002).

3.5. Region 4 – Central Europe

The region lies in the "centre" of the European subcontinent, between Western and Eastern Europe. The eastern border roughly follows the basins of rivers originating in the Carpathians. The northern part of the region was repeatedly subjected to glaciations during the Middle and Late Pleistocene, which were particularly strong in the MIS16 and MIS12 stages (Fig. 7A).

The Carpathian mountain range extends in the form of an arc in the latitudinal and longitudinal directions, framing the Great Hungarian Plain (= Pannonian or Carpathian Basin). The Carpathians are bordered to the north-west by the Tatra Mountains and to the south by the Transylvanian Alps. In the Pleistocene, mountain glaciations covered

only small areas of the highest places of the mountain ranges (Zasadni and Klapýta, 2014).

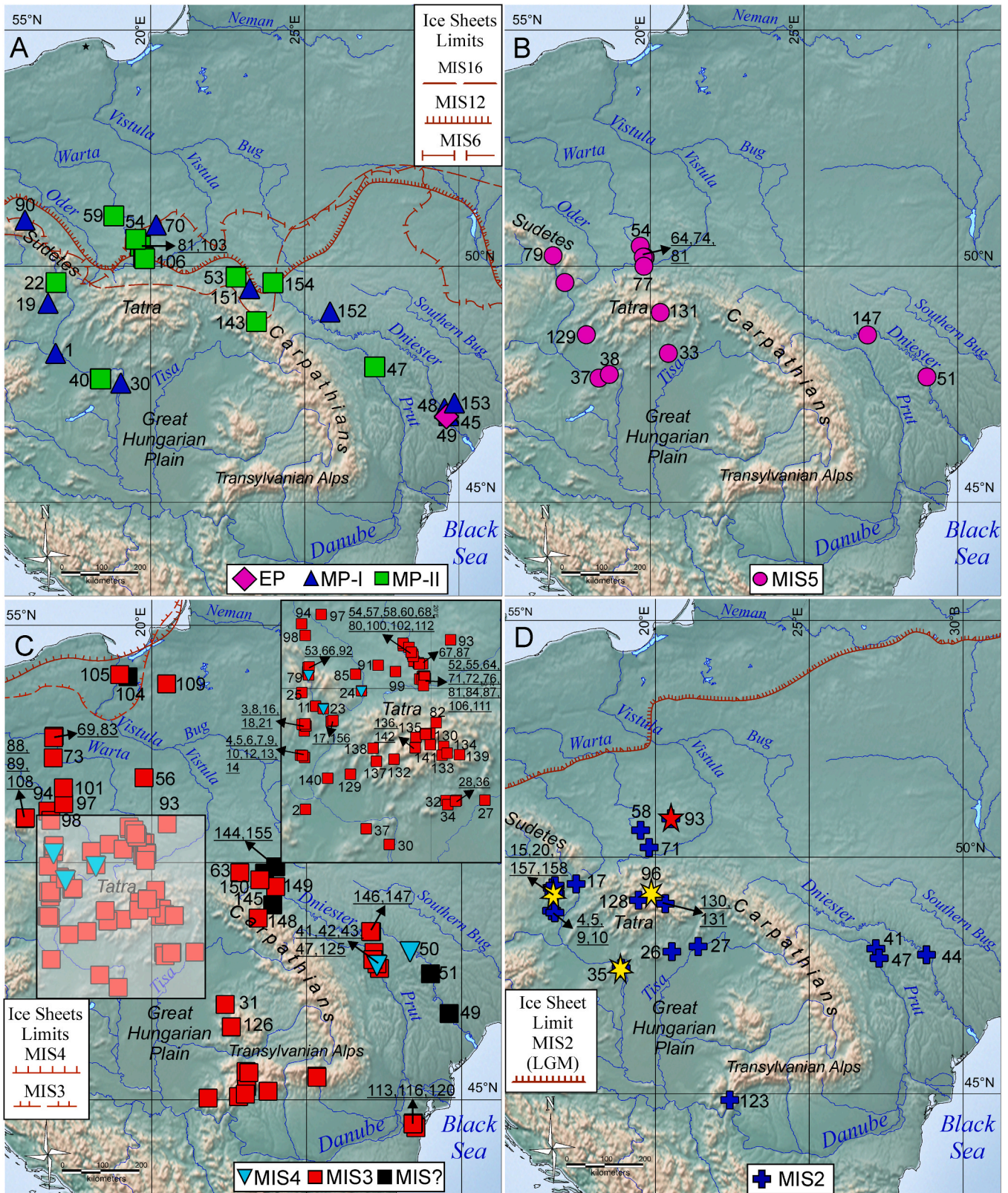
The oldest finds of cave lions in this region have not been instrumentally dated. There are evidence of the possible presence of lions at the end of the EP time window in the lower reaches of the Dniester (Tiraspol, Moldova) (Fig. 7A) and in its middle reaches at the beginning of MP-I (Sinyakovo 1, Ukraine) (Vereshchagin, 1971). The fossils from the Kozi Grzbiet (Poland) dated in the range of MIS19–MIS17 (Marciszak et al., 2021) and from the Stránská skála Cave (South Moravia, Czech Republic) probably belong to the glacial of MIS18 (Thenius, 1972; Kučera et al., 2009).

The MP-I sites are mainly located north-west of the Carpathians, in the Tatra's region and Transdanubian Mountains. The younger sites (MP-II, LP) are also concentrated in these areas, but they occur in the Pre-Carpathian region, in the upper Dniester basin (Figs. 7A, 7B). In general, sites are very unevenly distributed throughout the region, both in the Middle and Late Pleistocene. For example, the absence of the species in the Great Hungarian Plain and on the south-western slopes of the Carpathians is characteristic, and in the Transylvanian Alps the lion is not recorded before MIS3.

The largest number of sites with cave lions was dated to the interstadial MIS3 (Fig. 7C). The species was distributed practically from the Black Sea coast to the Baltic Sea coast.

In the early LGM there was a significant decrease in the number of sites (Fig. 7D). The youngest date of 27722–27288 cal years BP (Poz-58067) derived from a lion bone is from Raj Cave (Poland) (Marciszak et al., 2021).

The 15 younger dates are derived from the remains of associated fauna and are therefore not very reliable due to the redeposition of remains observed in many Central European caves. Approximately 46 % of these dates fall within the 27000–25000 cal years BP interval and 27 % each within the 25000–20000 and 18000–16000 cal years BP intervals, respectively. In summary, we believe that the cave lion became extinct in the region no later than the end of the LGM (GS-2.1a).



(caption on next page)

Fig. 7. The sites with cave lion remains in the Region 4 – Central Europe; the sites with the youngest cave lion remains dated directly (red asterisk) or indirectly (yellow asterisk) are marked: 1 – Deutsch-Altenburg 1, 2 – Windener Bärenhöhle, 3 – Sobolova (Barová) Jeskyně, 4 – Dolní Věstonice I, 5 – Dolní Věstonice II, Ila, 6 – Dolní Věstonice III, 7 – Dolní Věstonice XVI, 8 – Feryho Tajná Cave, 9 – Milovice I, 10 – Milovice IV, 11 – Mladeč cave 1, Lautscher Höhle, 12–14 Pavlov I, II, VI, 15 – Pekárna Cave, 16 – Pod Hradem Cave, 17 – Předmostí, 18 – Sloup-Šošůvka Caves, Slouper-Höhle, 19 – Stránská skála Jeskyně, 20 – Švédův stůl, 21 – Výpustek Cave, 22 – Za Hájovnou Cave, 23 – Kůlna Cave, 24 – Šipka, 25 – Srbsko-Chlum komín, 26 – Balla Cave, 27 – Bodrogkeresztúr (Henye Hill), 28 – Budaspes, 29 – Castle Hill, 30 – Érd, 31 – Igric (Igrita) Cave, 32 – Istállóskó Cave, 33 – Kalman Lambrecht Cave, 34 – Peskő Icave, Petényi Cave, 35 – Píliszántó, 36 – Szeleta Cave, 37 – Tata-Porhanyó báya, Porhanyó Quarry, 38 – Tokod, Tokod-Nagyberek, 39 – Vértesszöllős I, 40 – Vértesszöllős II, 41 –Bránzeni, Brynzeny-Tsyganka, 42 –Butești, 43 – Buzduzhany 1 (Buzdujeni I Cave), 44 – Climăuți II, 45 – Kolkotova balka, 46 – Malaeshty quarry, 47 – Duruitoarea Veche, Starye Durutory, 48 – Sukleya, 49 – Tiraspol, 50 – Trinka I-III, 51 – Vyhvatintzy grotto, grota Ofatintzi, 52 – Bęłowska Dolna Cave, 53 – Biały Kamień Cave, 54 – Biśnik Cave, 55 – Borsuczka Cave, 56 – Brzeziny, 57 – Cave no. on Mount Górze Birów, 58 – Deszczowa Cave, 59 – Draby 3, 60 – Dziadowa Skala Cave, 61 – Dzierzgoń, 62 – Głuszycza Górna, 63 – Hureczko, 64 – Cienna Cave, 65 – Magurska Cave, 66 – Cave in Rogóźce, 67 – Jasna in Strzegowej Cave, 68 – Komarowa Cave, 69 – Kowanówko, 70 – Kozi Grzbiet, 71 – Koziarnia Cave, 72 – Koziarnia Cave, 73 – Krakowska Cave, 74 – Łokietka Cave, 75 – Mały Baldram, 76 – Jaskinia Maszycka, 77 – na Gołąbcu Cave, 78 – Naciekowa Cave, 79 – Niedźwiedzia Cave, 80 – Niedźwiedzia Górna Cave, 81 – Nietoperzowa Cave, 82 – Oblazowa Cave, 83 – Oborniki, 84 – Ojców, 85 – Pawłowiczki, 86 – Perspektywiczna Cave, 87 – Pod Stupami Cave, 88 – Pólnocna Duża (Great North) Cave, Witschelhöhle, 89 – Połom Góra, Caves of Połom Mountain, 90 – Południowa Cave, Kitzelhöhle, Teufelskeller, 91 – Pyskowice, 92 –Radochowska Cave, 93 – Raj Cave, 94 – Rakoszyce, 95 – San River, 96 – Sąspowska Wschodnia Cave, 97 – Skarszyn, 98 – Sobótka, 99 – Sosnowiec–Milowice, 100 – Stajnia Cave, 101 – Szkaradowo, 102 – Towarna Cave, 103 – Tunel Wielki Cave, 104 – Waplewo Wielkie, 105 – Węgry, 106 – Wierchowska Górna Cave, 107 –Witków, 108 – Wojcieszów, 109 – Zamkowa Dolna Cave, 110 – Zawalona Cave, 111 – Zbójcka Cave, 112 – Zegar Cave, Clock Cave, 113 – "La Adam" Cave, 114 – Bordul Mare d'Ohaba Ponor, 115 – Borošteni Pestera, Cioarei à Borošteni, 116 – Cheia La Izvor, 117 – Pestera Cioclovina Uscata, 118 – Closani Cave, 119 – Liliacilor, Mare de Moieciu, 120 – Peștera Bursucilor, 121 – Peștera Cioarei, 122 – Peștera cu Oase, 123 – Grota Haiducilor, Peștera Hoților de Băile Herculane, Cave of the Thieves, 124 – Peștera Muierii, Muierillor de Baia de Fier, 125 – Ripiceni-Izvor, 126 – Urșilor Cave, 127 – Valea Coacăzei, 128 – Beșenová Báňa, 129 –Certova Pec, 130 –Dzeravá skála, Deravá skála, 131 – Gánovce-Hrádok, 132 – Harmanecká Jaskyňa, 133 – Koniarova Jaskyňa, 134 – Medvedia jaskyňa v Slovenskom raji, 135 – Medvedia Jaskyňa v Západných Tatrách, 136 – Okno, 137 – Prepošská Cave - Bojnice I, 138 – Pruziňská Dúpná, 139 – Sarkanova diera, 140 – Tmavá skála, 141 – Važecká Jaskyňa, 142 – Vyvieranie, 143 – Bilykh Stin Cave, 144 – Horodok, Gródek, 145 – Lisovychi, 146 – Molodova 1, 147 –Molodova 5, 148 – Perlyna, 149 –Pryima I, 150 – Rudky, 151 – Sambor, 152 – Sinyakovo 1, 153 – Velyka Mykhailivka, Grosulovo, 154 – Vynyavy, 155 – Volia-Homuletska, 156 – Hlavicova Cave, 157 – Kateriňská Cave, 158 – Sloupsko-šošovské Cave.

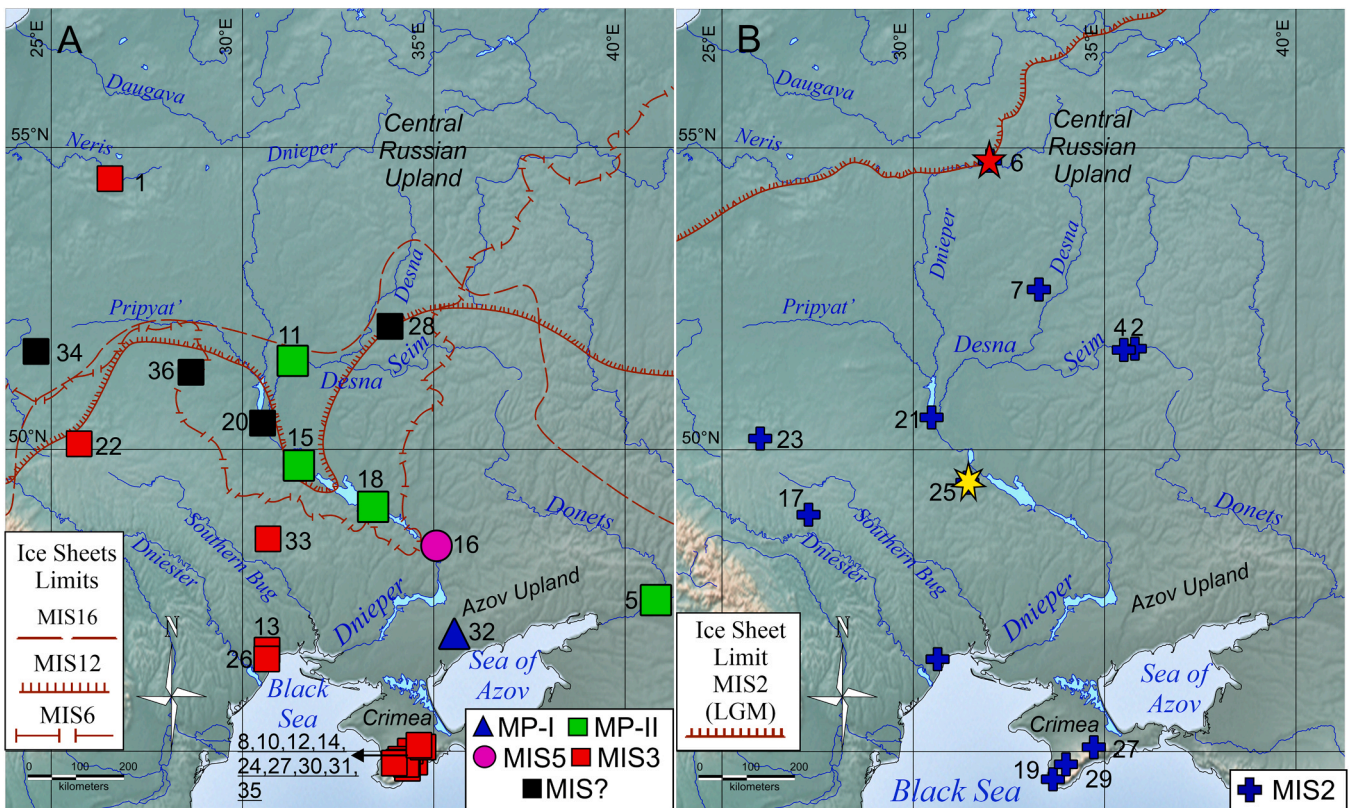


Fig. 8. The sites with cave lion remains in the Region 5a – East European (western part); the sites with the youngest cave lion remains dated directly (red asterisk) or indirectly (yellow asterisk) are marked: 1 – Smorgon', 2 – Avdeevo, 3 – Bol'shaya Shat'ma, 4 – Byki 1, 5 – Semikarakorskaya, 6 – Smolensk Region, 7 – Yudinovo, 8 – Adzhi-Koba, 9 – Buran-Kaya-III, 10 – Chagorak-Koba, 11 – Chernihiv, 12 – Emine-Bair-Khosar Cave, 13 – Il'inka, Illinka, 14 – Kabazi II, 15 – Kaniv, 16 – Kodak 1, 17 – Kormaniv, 18 – Kremenchug, 19 – Kryshataleva Cave, 20 – Kyiv, 21 – Kyrylivska str., Kyiv, 22 – Kulichivka, 23 – Lipa IX, Mala Ilovytsya, 24 – Marmurova Cave, 25 – Mezhyrich, 26 – Odessa-Nerubaj Caves, 27 – Prolom II, 28 – Romankove, 29 – Shaitan-Koba (Bodrak), 30 – Suren Cave 1, 31Suren Cave 2, 32 –Tykhonivka, 33 – Volodymyrivka, 34 – Volyn, 35 – Zaskalna VI (Kolosovskaya) Cave, 36 – Zbranky.

3.6. Region 5a – East Europe, western part

The region includes the Dnieper River basin with its tributaries, the Southern Bug River basin and the Crimean Peninsula (Fig. 8). The relief

is flat with not high uplands. Relatively low mountains situated in the south of the Crimea ("Mountainous Crimea"). The eastern boundary of the region is drawn along the basin of the Donets River, and then northwards along the watershed between the Dnieper and Volga Rivers,

approximately, across the Central European Uplands. During the Middle Pleistocene, more than half of the region was subjected to cover glaciation (Ehlers et al., 2013a). In the Late Pleistocene, the ice sheet covered only the northern part of the region (Ehlers et al., 2013b).

The total number of known cave lion sites in this region is small compared to the western and central European regions discussed above. In our opinion, this fact cannot be interpreted as evidence of the rarity of cave lions here. The prevalence of this carnivore is indirectly indicated by the high concentration of finds in the Mountain Crimea, i.e. in cave sediments, which are more favourable for the preservation of fossil remains. On the plain, lion remains are usually restricted to alluvial deposits of large rivers and/or open-air hominid sites.

Only five Middle Pleistocene (MP-I, MP-II) sites are known. The oldest of these, Tykhonevka (= Tikhonovka), is located in the south of the region (Pidoplichko, 1956) (Fig. 8A), corresponds to the MIS16 stage according to its stratigraphic and zoological characteristics (Krokhmal, 2014). The northernmost Middle Pleistocene site, Chernihiv (= Chernigov), is located at latitude ~51°29'8"N (Tatarinov, 1969).

The Middle Palaeolithic site of Kodak 1 is probably the only in the region that can be dated to the Eemian (= Mikulino) Interglacial, located in the lower reaches of the Dnieper River (Fig. 8A).

Late Pleistocene finds are also scarce. There are three direct radiocarbon dates in the interval from 63104–52798 years BP (OxA-17044, Emine-Bair-Khosar Cave, Crimea) to 17342–16966 years BP (OxA-17034, Smolensk District, upper Dnieper River) (Stuart and Lister, 2011). The young indirect dates obtained for *Mammuthus primigenius* tooth and burned bone from the Mezhyrich (= Mezhirichi) locality in the middle reaches of the Dnieper River are 15411±321 (OxA-0709, maybe

too young date) and 21839±723 cal years BP (KI-1055) (Gowlett et al., 1987; Lorenzen et al., 2011) (Fig. 8B).

There is also a series of nine relatively young dates on mammoth bones from the lower cultural layer of the Yudinovo site (Russia) with an average value of 16049.9±260.9 cal years BP (Gavrilov et al., 2004).

According to the available data, the cave lion disappeared from the region at the latest during the first part of the deglaciation phase or earlier, at the end of the LGM (GS-2.1b-a).

Within the interval 29–17 ka BP (MIS2), there is a negative correlation ($r = -0.60, p = 0.049, N = 11$) between latitude and radiocarbon dates. This may indicate that the process of species range reduction began from the south and then spread to the north in this region, rather than from the north to south, as we described above for western or central Europe.

3.7. Region 5b – East European, eastern part

The easternmost of the European regions identified in this study lies between the Dnieper and Volga basins. Its eastern boundary follows the course of the Volga River, the Kama River (a tributary of the Volga) and, further north, the west of the Ural Mountains. During the Middle Pleistocene, glaciers repeatedly covered the region. A particularly large glaciation is associated with MIS16 stage (Don Glaciation) (Fig. 9A), which was the most extensive on the Eastern European Plain as well as in the rest of Europe. During the LGM, the region was almost unaffected by cover glaciation.

We have relatively little evidence for the presence of cave lions in this region. Moreover, for the Middle Pleistocene we can only infer their

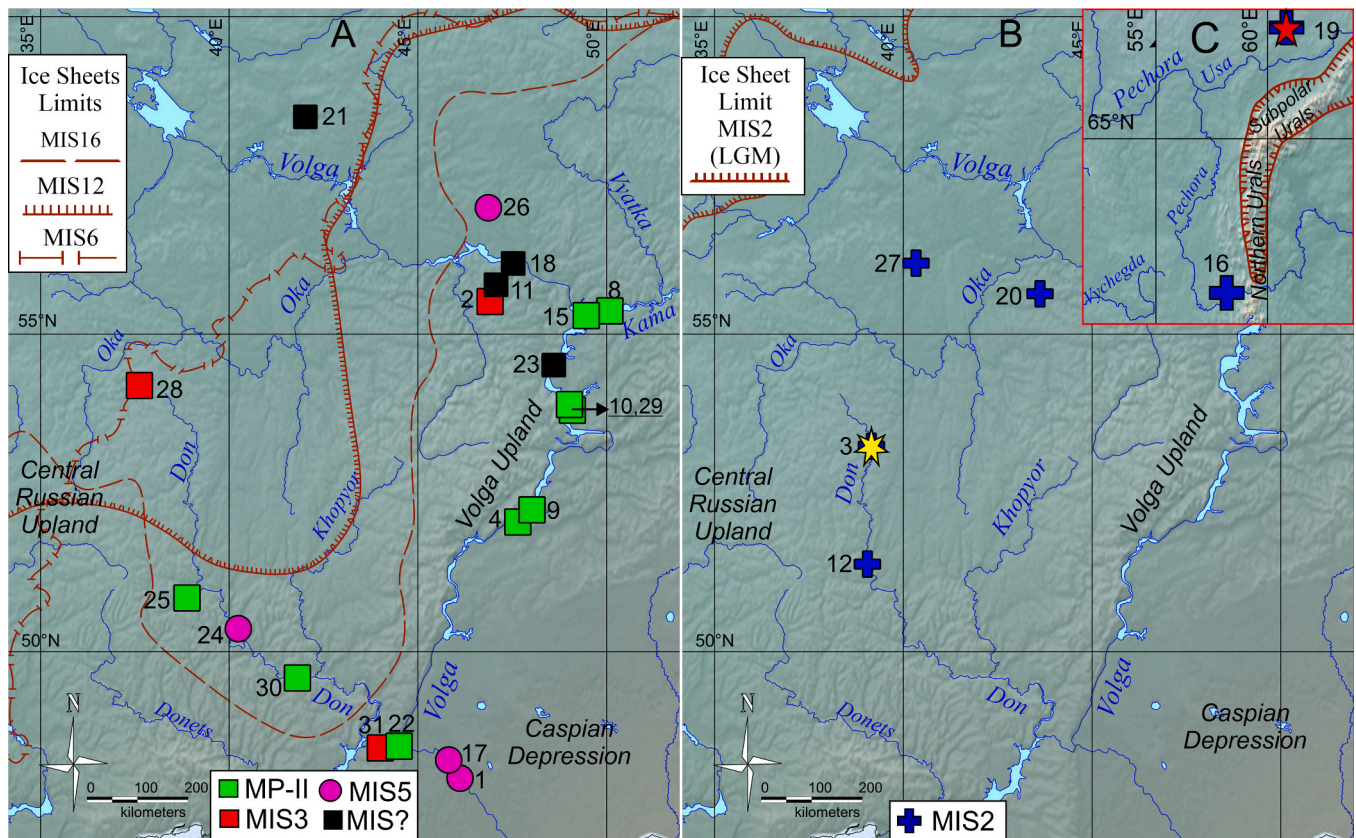


Fig. 9. The sites with cave lion remains in the Region 5b – East European (eastern part); the sites with the youngest cave lion remains dated directly (red asterisk) or indirectly (yellow asterisk) are marked: 1 – Chernyi Yar, 2 – Bolshaya Shat’ma, 3 – Dyad’kovo site, 4 – Devich’ya Gorka, 5 – Dinamitnaya, 6 – Geologolov-3 Cave, 7 – Ivaka Grotto, 8 – Kama River, 9 – Khoroshovski Island, Volga River, 10 – Khrayshevka, 11 – Koshki, 12 – Kostenki I (Polyakova site), 13 – Kumyshanskaya Cave, 14 – Ladeinyi Kamen’, 15 – Mansurovo, 16 – Medvezh’ya Cave, 17 – Nizhnee Zaimishie, 18 – Novocheboksarsk, 19 – Pymva-Shor II, 20 – Pystyn’ 2, 21 – Rossolovo, 22 – Sarepta, 23 – Serdysh Island, Volga River, 24 – Shkurlat or ‘Shkurlat’s layers’, 25 – Shubnoe, 26 – Sobolevo or Kubashevsky, 27 – Sungir’, 28 – Tula, 29 – Tunguz Peninsula, Volga River, 30 – Veshenskaya, 31–Volga-Don channel.

presence for the MP-II time window (Fig. 9A), without association with any isotopic stage. The only instrumental date (TL) within the interval 200–185 ka BP (MIS7–MIS6) was obtained for the fluvial deposits of the Veshenskaya site on the Don River, but it should be treated with caution (Baygusheva et al., 2014). Note that seven of the nine Middle Pleistocene sites are north of 50°N.

The MIS5 stage was dated for four sites in both the south and north of the region (Fig. 9A).

The confidence interval of the four direct dates is 33327–15270 cal years BP. Cave lion remains in MIS2 are mostly located between 51°N and 57°N, and two sites (Medvezh'ya Cave and Pymva-Shor II), are located north of 62°N (Fig. 9B).

The youngest indirect dates on *Saiga tatarica* and *Coelodonta antiqutatis* bones are 16100±120 (AAR-11393) and 15210±98 (GIN-9503) cal years BP, respectively, were obtained from sites located at 59°10'12"N (Ivaka Grotto) and 53°15'6"N (Dyad'kovo site).

The Pymva-Shor II site is located at 67°9'58.5"N (Pechora River basin, Subpolar Urals, Russia) and it is the northernmost cave lion site in Europe. The cave lion remains from this site are the youngest for the region and dated within interval 15814–15270 cal years BP (Ua-14006) (Kosintsev et al., 2016).

It is therefore likely that the species went extinct in this region after the LGM, somewhere in the time interval corresponding to the Oldest Dryas (GS-2a).

3.8. Region 6 – Caucasus and Middle East

Region 6 is particularly important in the history of the cave lion, as it is the most likely route by which the ancestors of this evolutionary lineage moved from Africa to Eurasia (if we accept the hypothesis of the African origin of *P. spelaea* s.l.).

The oldest remains from the south of the region identified as belonging to a cave lion came from Hummal (El Kowm, Syria) (Elsuede and Savioz, 2017) and Bear's Cave (Israel) (Tchernov and Tsoukala, 1997) (Fig. 10A) Their ages were determined to range from MIS9 to MIS7 stages. On the northern macroslope of the Greater Caucasus, in Treugol'naya Cave (Russia), cave lion remains have been described (Hoffecker et al., 2003) in layers (7a, 6, 4b) dated (ESR) in the range from about MIS15 (Molodkov, 2001) to MIS13 and MIS10, respectively

(Blackwell et al., 2005). Note also the Middle Pleistocene Emirkaya-2 locality (Turkey) with an age determined from the associated fauna corresponding to the MIS11 interglacial (Sen et al., 1991; Kessler and Venczel, 1993).

In the Late Pleistocene, in the south of the region, two sites, Dederiyeh and Douara Cave (Syria), have dates (TL) of 70–50 ka BP and 75 ka BP, respectively (Hanihara and Akazawa, 1987; Griggo, 2004) (Fig. 10B).

Most Late Pleistocene sites are concentrated within the Caucasus region. The species inhabited the Caucasus up to and including the MIS2 stage (only indirect dates are available). The youngest date (13570 ±93 cal years BP, OxA-7853) was obtained for layer 1 of the Sakajia (= Sakadgia) Cave (Georgia) (Nioradze and Otte, 2000) (Fig. 10B).

Available data indicate that the extinction of the cave lion occurred before the Younger Dryas (GS-1) in the northern part of the region. In the south, the latest dates of 46.8 cal ka BP (MIS3) have been obtained from Douara Cave (Hanihara and Akazawa, 1987).

3.9. Regions 7 – Western Siberia

The West Siberian region occupies the southern part of the West Siberian Plain. Its border runs roughly along the northern edge of the Kazakh Uplands, and its eastern border is along the Yenisei River basin. The Ural Mountains lie to the west of the region.

During the Middle–Late Pleistocene, the area to the north of the region was subject to glaciation, with the greatest extent during MIS8 and MIS6, and the least during the MIS2 stage (LGM). According to V.I. Astakhov (Astakhov, 2019), the boundary of the maximum glaciation in Western Siberia was more southerly than that shown in Fig. 11A. The position of the northern boundary of the West Siberian region corresponds approximately to this line.

The mandible described from Sagarlyk Formation of the Bachatsk Quarry (Russia) on the east of the West Siberian region, belonged to member of the cave lion lineage (*P. fossilis*) and is one of the oldest of the cave lion remains in Eurasia (Sotnikova and Foronova, 2014). The sediment formation in which it was found was dated to the Jaramillo Subchron, i.e. to interval of MIS30–MIS28, according to various estimates. Two other sites (alluvial deposits) with cave lions remains are not precisely dated and probably belonging to the MP-I time window. They

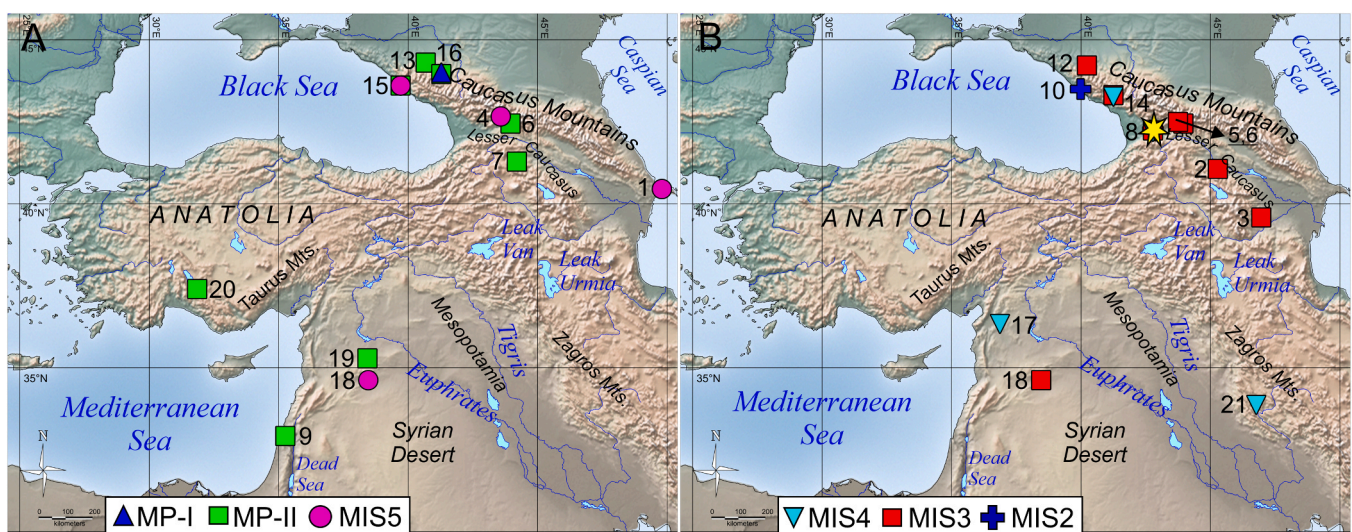


Fig. 10. The sites with cave lion remains in the Region 6 – Caucasus and Middle East; the site with the youngest cave lion remains dated indirectly (yellow asterisk) is marked: 1 – Binagady, 2 – Dash Salahli, 3 – Taghlar Cave, 4 – Bup Cave, 5 – Kudaro Cave 1, 6 – Kudaro Cave 3, 7 – Kvemo-Orozmani, 8 – Sakajia, 9 – Bear's Cave, 10 – Achshtyrskaja or Ahtyrskaya Cave, 11 – Chasovali Hoh, 12 – Dakhovskaya Cave, 13 – Gubs River, 14 – Mezmaiskaya Cave, 15 – Bocharov Stream, 16 – Treugol'naya Cave, 17 – Dederiyeh, 18 – Douara Cave, 19 – Hummal, El Kowm, 20 – Emirkaya-2, 21 – Wezmeh Cave.

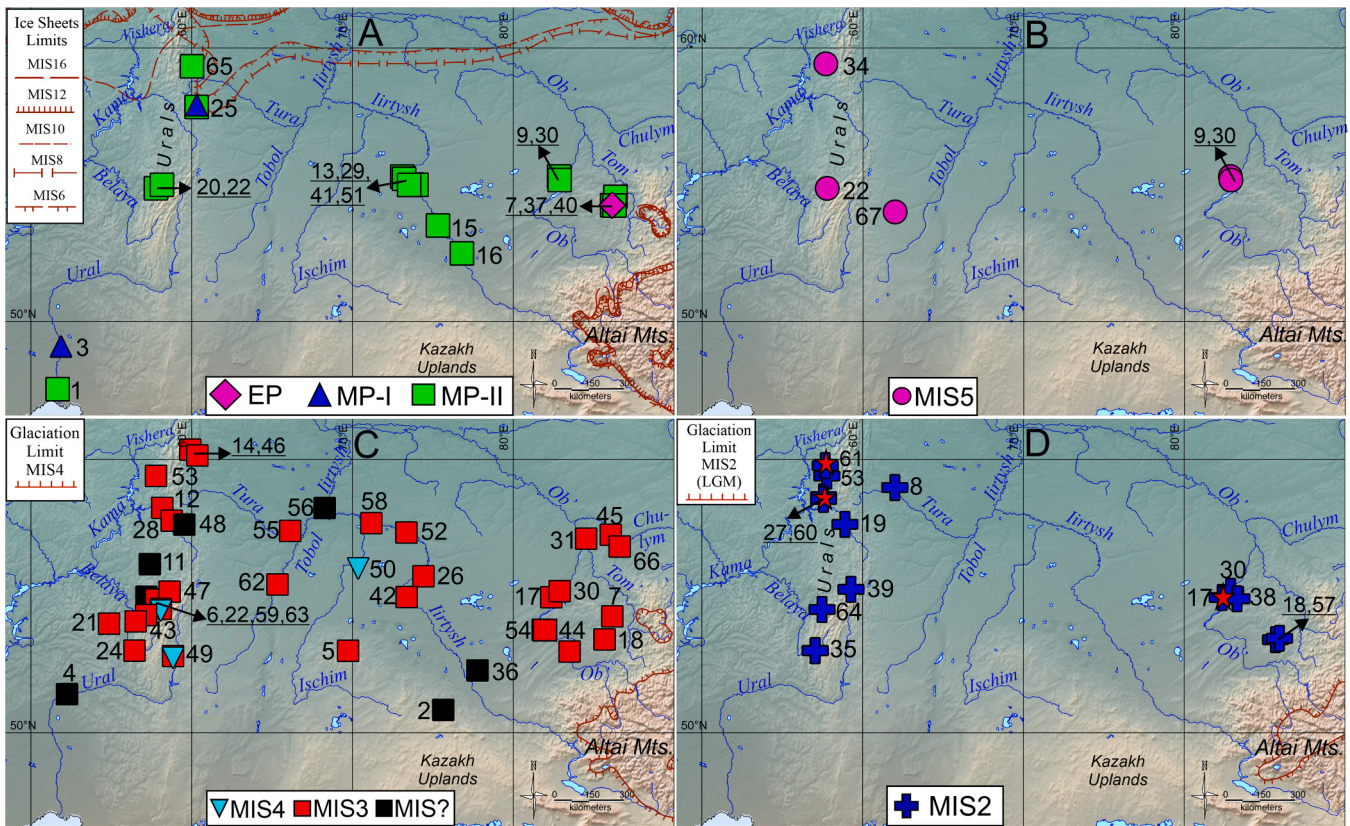


Fig. 11. The sites with cave lion remains in the Region 7 – Western Siberia; the sites with the youngest cave lion remains dated directly (red asterisks) are marked: 1 – Alebastrovo-Saraichik, 2 – Toraigr Lake, 3 – Ural River, 230 km from the mouth, 4 – Yanvartsevo, 5 – Aktas, 6 – Asha 1 (Kozya), 7 – Bachatsk Quarry (Shirta horizon, Sagarlyk Formation), 8 – Balakino, 9 – Bibikha, 10 – Bogoslovka 2, 11 – Bobilek, 12 – Bol’shoy Glukhoy Cave, 13 – Borki-Kornilovka, 14 – Cheremukhovo 1, 14 – Cheremukhovo 1, 14 – Cheremukhovo 1, 15 – Zhelezinka, 16 – Chernoyarka, 17 – Chick River, 18 – Chumysh Rever, between Martynovo and Kytmanovo, 19 – Dyrovaty Kamen’ (Tchusovaya River), Dyrovatyj-na-Chusovoj, 20 – Grebnevaya Cave, 21 – Idrisovskaya Cave, 22 – Ignat’evsky, Ignatievskaya Cave, 24 – Imanay Cave, 25 – Isa River, 26 – Isakovka, 27 – Kholodnyi Grotto, 28 – Kotel, 29 – Krasnojarka, 30 – Krasny Yar Village, Novosibirsk region, 31 – Krasny Yar Village, Tomsk region, 32 – Kul’jurt-Tamak Cave, 34 – Makhnevskaya Ledianaya Cave, 35 – Maksyutovo Grotto, 36 – Maraldy Lake, 37 – Mokhovo, 38 – Mosikha River, 39 – Nikol’skaya Cave, 40 – Novosergeevo, 41 – Novotroickoe 1, 42 – Omsk, 43 – Pobeda Cave, 44 – Priobskoye Steppe Plateau, 45 – Sergeevo, 46 – Shaitanskaya Cave, 47 – Sikiyaz-Tamak 7, “Kaminnaya”, 48 – Sisimka River, 49 – Smelovskaya 2 Cave, 50 – Spirino, 51 – Stepnoi, 52 – Tabory, 53 – Tain Cave, 54 – Taradanovo, 56 – Tobolsk, 57 – Togul River Basin, 58 – Ust’-Ishim, 59 – Ust’-Katavskaya Cave, 60 – Verkhnegubakhinskaya Cave, 61 – Viasher Cave, Kizelovskaya Cave, 63 – Zapovednaya Cave, 64 – Zhemchuzhnaya Cave, 65 – Zhilische Sokola, 66 – Zyryanskoe, 67 – Zyuzelga River.

locate in the basins of the Ural River and Isa River (a tributary of the Irtysh River) (Fig. 11A). The latter site is the northernmost (57°52’30’’N) for the Middle Pleistocene in the region.

In general, the region has a relatively high number of Middle Pleistocene lion sites dated between MIS11 and MIS6 (MP-II).

The MIS5 dated sites form two geographical groups – in the Altai foothills (Ob’ River basin) and in the Southern Urals (Fig. 11B). The northernmost of these (Makhnevskaya Ice Cave) is located at latitude ~59°27’N.

Based on the spatial distribution of localities in the MIS3 stage, we can assume that the cave lion was widely distributed between the Altai foothills and the Ural Mountains during this time (Fig. 11C). The northernmost sites, Cheremukhovo and Shaitanskaya Cave, are located in the Ural Mountains at latitudes 60°22’42’’N and 60°10’1’’N, respectively.

From Western Siberia and the Urals 27 radiocarbon dates are known for cave lion remains in the interval from 55301 to 15941 cal years BP.

In the Ural region, the dates obtained from cave lion remains range from 55 to 16 cal ka BP. The youngest dates come from the Verkhnegubakhinskaya Cave (16607–16142 cal years BP, OxA-10909) and the Viasher Cave (16620–16159 cal years BP, OxA-10908) (Stuart and Lister, 2011).

In the Irtysh River basin, direct dates exceed 50 cal ka BP, and indirect dates range from 44 to 16 cal ka BP.

In the Ob’ River basin, in the southeast of the region (Fig. 11C, D), the ages of cave lion remains range from 55 to 15 cal ka BP. Most of them are dated to the MIS3 stage. The youngest lion remains from the Altai foothills (Chick River) dated to the interval 16665–15223 cal years BP (BINP-NSU-1306) (Vasiliev et al., 2018).

Given the low reliability of indirect dating from the remains of associated fauna from alluvial deposits, we did not show these sites in Fig. 11D. However, these sites, potentially associated with MIS2, are listed in the supplementary material database (Table S9).

Thus, based on the available data, we can conclude that the cave lion became extinct in the region between ~17 and 15 cal ka BP, not later than the end of the Oldest Dryas cooling (GS-2a). It is possible that the lion disappeared from the Irtysh River basin much earlier, during the MIS3 isotopic stage.

3.10. Region 8 – South Siberia and Middle Asia

The region includes the Altai-Sayan Mountains and the Baikalia and Transbaikalia areas.

Cave lion finds in Central Asia, western Tien Shan, are considered within the same region (Fig. 12B). There is modern mountain glaciation in the region (Kotlyakov et al., 1993). The compositions and extents of Pleistocene glaciations in the region are under debate (Okishev, 2011). Fig. 12 shows the wide distribution of mountain glaciers in different

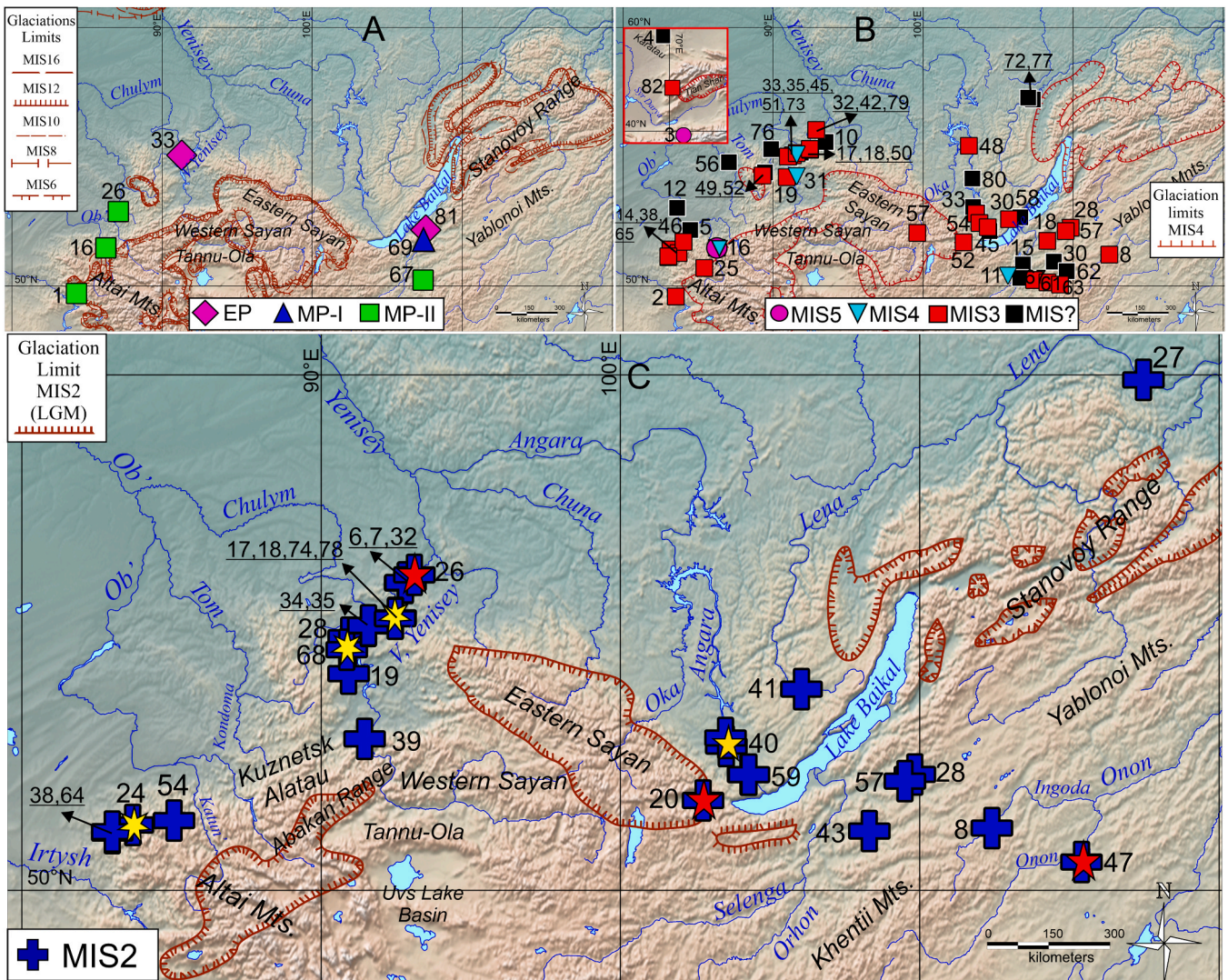


Fig. 12. The sites with cave lion remains in the Region 8 – South Siberia and Middle Asia; the sites with the youngest cave lion remains dated directly (red asterisks) or indirectly (yellow asterisks) are marked: 1 – Zryanovsk, Parygina mine, 2 – Bukhtarma (= Bukhtarminskaya Cave), 3 – Sel'-Ungur Cave, 4 – Ushbas Cave, 5 – Anui R., 6 – Afontova Gora II, 7 – Afontova Gora V, 8 – Arta 2, 9 – Baday-II, 10 – Belyi gorod, 11 – Botsiy, 12 – Buranovo, 13 – Buret', 14 – Chagyrskaya Cave, 15 – Chikoi R., 16 – Denisova Cave, 17 – Derbina 4, 18 – Derbina 5, 19 – Dvuglazka, Glyadeny, 20 – Elovka, 21 – Gorohovo, 22 – Gorome-1 Cave, 23 – Kamenka, 24 – Kaminnaya Cave, 25 – Kara-Bom, 26 – Kedrovka, 27 – Khayrgas Cave, 28 – Khotyk 3, 29 – Kokorevo II (Telejnyi log), 30 – Kondabaev 31 – Krasnoturansk, 32 – Kubekovo, 33 – Kurtak (Berezhkovo), 34 – Kurtak 3, 35 – Kurtak 4, 36 – Kurtun 1 Cave, 37 – Kyahta, 38 – Logovo Gieny Cave, 39 – Maininskaya = Mayna, 40 – Mal'ta, 41 – Malye Goly, 42 – Microdistrict Yasny, Krasnoyarsk, 43 – Nikolskaya, 44 – Novogrudinino, 45 – Novoselovo, 46 – Okladnikov Cave, 47 – Onon R., 48 – Ozernaya Balya, 49 – Petuhovskaya Cave, 50 – Pokrovka 2, 51 – Primorsk, 52 – Proskuryakova Grotto, 53 – Pshenichnaya, 54 – Razboinichya Cave, 55 – Roshcha Zvezdochka, 56 – Saltymakovo, 57 – Sannyi mys, 58 – Sagan-Zaba, 59 – Sedova, 60 – Shchapova 2, 61 – Shergol'dzhin, 62 – Shimbili, 63 – Stanchikovskiy Yar, 64 – Strashnaya cave, 65 – Strashnaya cave, 66 – Svirsk, 67 – Tamir, 68 – Tashtyik I, 69 – Tologoi 2, 70 – Titovo, 71 – Tuyana, 72 – Ul'kan, 73 – Ulazy, 74 – Ust'-Maltat I, 75 – Ust'-Odinskoe, 76 – Uzbur, 77 – Verhnamarkovo, 78 – Volchika II, 79 – Yasnoe 1, 80 – Yugolok, 81 – Zasukhino 382 – Obi-Rakhmat.

glacial periods of the Middle and Late Pleistocene. The lowest modelled extent of glaciers seems to have occurred during the MIS2 stage.

The altitude of the sites varies from 500 to 4500 m. a.s.l. in the Altai-Sayan Mountains and Transbaikalia, and up to 2000 m. a.s.l. in the Tien Shan Mountains.

The oldest sediments containing cave lion remains were found at the Zasukhino 3 site (Transbaikalia) and dated to the end of the Early Pleistocene (~MIS22) (Vangengejm et al., 1990). Lion remains of approximately the same age or slightly younger were found at the Kurtak site (Berezhkovo, pit 2, level 6) in the Yenisei River basin (Chlachula, 2001). In the Transbaikalia site Tologoi 2 (Tologoi 2.5–2.1 complex), cave lions were found in deposits dated to the early Middle Pleistocene above the Brunhes/Matuyama boundary (Ivanova et al., 2019).

The species was found in the famous Denisova Cave (Western Altai, Russia) in late Middle Pleistocene layers, for which dates (OSL) were obtained between ~356 and 139 ka BP (Jacobs et al., 2019). Evidence of cave lions inhabiting the region in the late Middle Pleistocene also came from the Kedrovka locality in the west and from the Tamir site in the east (Transbaikalia).

Fig. 12 shows a spatial hiatus between the groups of sites in the west and east of the region that persists from the Middle to Late Pleistocene. This gap is definitely associated with the position of the Eastern Sayan Mountains, extending approximately latitudinal between the Kuznetsk Alatau and Lake Baikal.

In the Central Asia, there are no records of a cave lion younger than ~43 cal ka BP and older MIS5 (?). The deposits of the Sel'-Ungur Cave (cultural layers 3–5) (Kyrgyzstan) are dated (U/Th) at 126000±5000 cal

years BP (Vishnyatsky, 1999). This is the southernmost (39°52'44.8''N) cave lion find in the region.

The Late Pleistocene is dominated by sites dated MIS3 (Fig. 12B) and MIS2 (Fig. 12C). We have 11 radiocarbon dates for lion remains in the region between 43453 and 21772/21762 cal years BP (Fig. 12C) (Stuart and Lister, 2011). Numerous dates for associated fauna (*Mammuthus primigenius*, *Ursus arctos*, *Lepus timidus*, *Equus* spp., *Bison priscus*, etc.) support the presence of lions here until the Bølling–Allerød and Younger Dryas (GI-1–GS-1) (Malikov et al., 2024).

It is likely that the species became extinct in Pribaikalia and Transbaikalia already at the end of the LGM (17985.0±210 cal years BP – average date for layer 8 of the Mal'ta locality, Angara River basin) (Vartanyan et al., 2008). However, in the west of the region, the cave lion could persist almost until the end of MIS2 (12526.7±353 cal years BP – mean date for layer 11 A, Kaminnaya Cave) (Kosintsev, 2010).

3.11. Regions 9 – Far East (Russia), China, Korean Peninsula

We included in this region the territory of the southern Russian Far East, the Korean peninsula, the territory of China up to the Great Khingan Range in the west and Beijing in the south-west. In general, the distribution of the cave lion in northeastern China and the adjacent areas bounded by the shores of the Yellow Sea and the Sea of Japan is unclear. A revision of the fossil remains of big cats, especially the "tigers", is needed and has been misidentified (Sherani et al., 2023).

To date, only five sites with cave lion remains are known here (Fig. 13). Among them, three localities are of Middle Pleistocene age in China and South Korea: Zhoukoudian, Locality 1 (layers 1–2, locus H) – MIS11 (Sotnikova and Foronova, 2014; Shen et al., 2001), Songhua River near Harbin – MIS10–MIS8 (Malikov et al., 2024), and the Kum Cave (South Korea) – end of the Middle Pleistocene (~MP-II) (Chung, 1989). The other three sites dated to the late Pleistocene. There are no direct dates for lion remains from these localities, but radiocarbon dates

on associated fauna (*Cervus* sp., *Crocota* sp.) from the Geographical Society Cave (Russia) and the Chongphadae Cave fall in the second half of MIS3 (Baryshnikov, 2016; Choe et al., 2020).

3.12. Region 10 – Eastern Siberia

The vast East Siberian part of the cave lion's range extended east-northeast from the Yenisei Basin to the shelf of the modern Arctic seas – the Laptev Sea and the East Siberian Sea (Fig. 14). Part of the area east of the Verkhoiansk Ridge belongs to the so-called Beringia, which also includes the territory of Alaska up to the Mackenzie River basin in northwestern Canada (Sushkin, 1925). Beringia is important territory for the evolution of cave lions in both Asia and North America.

Mountain and cover glaciations in the region were common during the Middle and Late Pleistocene, especially in the northeast and northwest (Fig. 14). It is likely that they could periodically create barriers between different parts of the cave lion's range.

Practically the entire territory of the region lies in the zone of continuous permafrost or of local permafrost (in the south), which is still spreading today. In the north, the so-called edoma, organic carbon-rich permafrost formed in the Late Pleistocene, is widespread in the region. Fossils including mummified bodies recovered from edoma are usually well preserved. Unique finds also came from this territory, allowing details of the morphology and biology of the cave lion to be reconstructed (Chung, 1989).

The earliest evidence for the presence of members of the cave lion lineage comes from Beringia from sediments of the Adycha River (near Ulakhan Sullar site, Yana River basin) and Berezovka River (Kolyma River basin) (Fig. 14A). According to the associated fauna, they are dated to the first half of the Middle Pleistocene (Baryshnikov and Boeskorov, 2001; Vereshchagin, 1971). Fossils of cave lions dated very roughly to the Early Middle Pleistocene (MP-I time window) have been obtained from the Yenisei Basin (Lower Tunguska River), the Vitym and

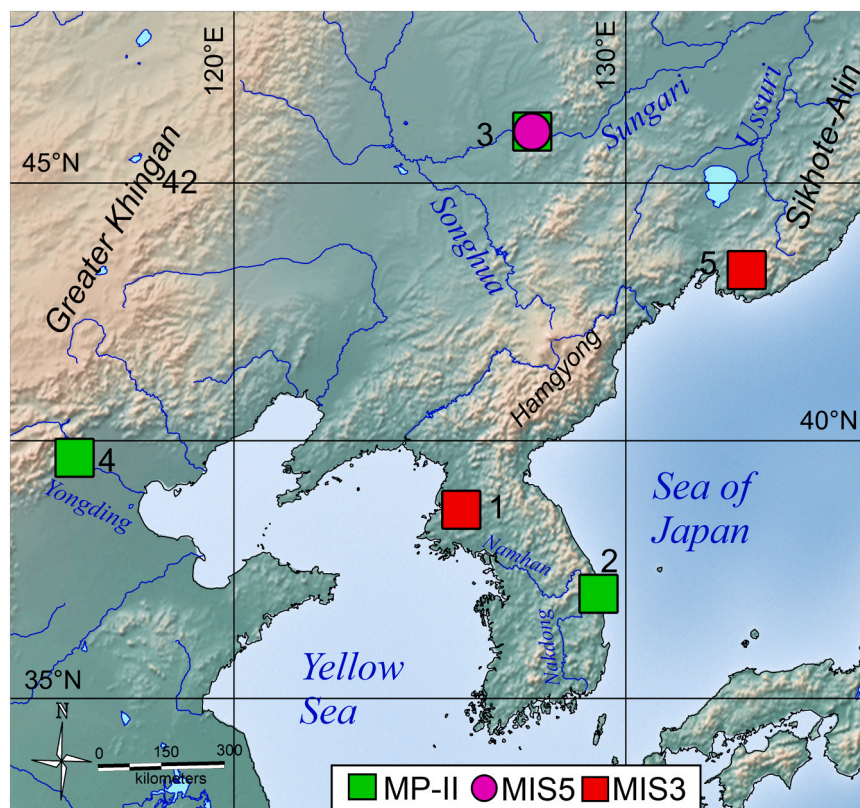


Fig. 13. The sites with cave lion remains in the Region 9 – Far East (Russia), China, Korean Peninsula: 1 – Chongphadae Cave, 2 – Kum cave site, 3 – Songhua River, 4 – Zhoukoudian Locality 1, 5 – Geographical Society Cave.

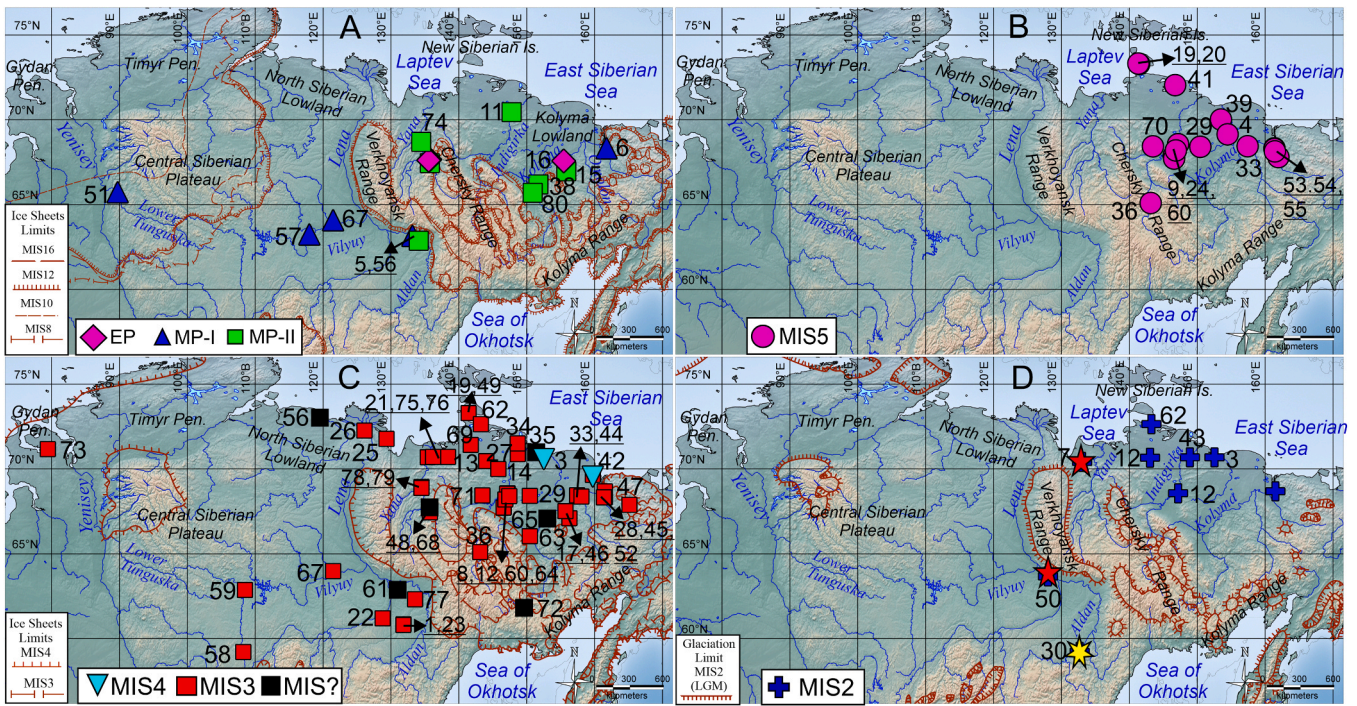


Fig. 14. The sites with cave lion remains in the Regions 10 – Eastern Siberia during the Middle–Early Pleistocene; the sites with the youngest cave lion remains dated directly (red asterisks) or indirectly (yellow asterisks) are marked: 1 – "Gora Korolenko", 2 – Adycha River, 3 – Alazeya River, 4 – Andryushkino, Alazeya River, 5 – Mamontovaya Gora, Aldan River, 6 – Anuysk, Lake Anuy, 7 – Arga-Yurekh River, 8–10 – Badyarikha River, 11 –Bayagnyr, 12 –Belaya Gora, 13 – Berelekh geochronological complex, Berelekh River, 14–16 –Berezovka River, 17 – Mayachnyy Ccreek, Berezovka River, 18 – Betenkes, 19 – Bol'shoy Lyakhovskiy Island, 20 – Zimovye River Basin, Bol'shoy Lyakhovskiy Island, 21 – Bulgunyakhtakh, Lena River Basin, 22 – Buotama River, 3 km from mouth, 23 – Chakyr, Amga River, 24 – the creek, left tributary of Ogorokha River, 25 – Mamontovy Khayata, Bykovskiy Peninsula, 26 – Kurungnakh Island, Lena River. Delta, 27 – Dolganov Lake, 18 km northwest of the Nychalah village (Byannyr), 28 – Gold field "Drevniy", Drevniy Creek, 29 – Duvanny Yar, 30 – Dyuktai Cave, 31 – "Eastern Siberia", 32 – "Easter Yakutia", 33 – Enge-Yuryue Site, 34 – Keremesit R. lower Indigirka River, 35 – Indigirka River Delta, 36 – the mouth of the Tirektyakh Creek, Indigirka River, 37– Indigirka R., upstream of Chokurdakh, 38 – Irelyakh-Siene River, 39 – Khomus-Yuryakh Bolshoy River, 40 – Khroma River, 41– Khaptashinskiy Yar, Khromskaya Guba, 42 – Chukochya River, 43 – Kondakovka River (downstream), 44 – Krestovka River, 45 – Stanchikovskiy Yar, Kolyma River, 46 – Vetrennyy Creek, Kolyma River, 47 – Konstantinovskiy Yar, 48 – Kyra Sullar, 49 – Kyttyk Peninsula, 50 – "Lena River", 51 – Lower Tunguska River, 52, 53 – Maly Anyuy River, 15 km and 17 km upstream from Anyuysk, 54 – Maly Anyui River, 56 – Mokkhokho, 57 – Naleskaya terrace, Vilyuy River, 58 – Nepa, 59 – Nizhnyaya Tunguska River, 60 – "Ogorokha" site, Ogorokha River, 61 – Oner Lake, 62 – Oyagossky Yar, 63 – Loc. 527, Sededema River, 64 – Semyuelyakh River, 65 – Slezovka, Kolyma River, 66 – Tandinskyy outcrop, Aldan River, 67 – Tyung River, 68 – Ulakhan Sullar, 69 – Uryung Uulaah Lake, 70 – Uyandina-2, Uyandina River, 71 – Uyandina-3, Uyandina River, 72 – Vetreny, Kolyma River, 73 – Yambuto Lake, Gydan Peninsula, 74 – Yana River, 75 – Kazach'e village, Yana River, 76 – RHS Site, YMAM (Yana Mass Accumulation of Mammoths), Yana River, 77 – Ytyk-Kyuel, 78 – Bunge-Toll site, Yungen Creek, 79 – Yunyugen, Yana River, 80 – Zyryanka.

Aldan Rivers (tributaries of the Lena River), and the Kolyma River Basin (Vereshchagin, 1971). Fossils from sediments of later age are found mostly within the Beringia area (Fig. 14A), with the exception of the Mamontovaya Mountain locality in the Aldan River Basin (Boeskorov et al., 2012). Among them there are several for which specific dates (OSL, U/Th) were obtained in the range from 360 to 176 ka BP (MIS11–MIS6). It should be noted that Middle or Late Pleistocene remains of cave lions were not found directly on the Chukotka Peninsula (not shown in Fig. 14).

Quite numerous lion remains, which are tentatively correlated here with the MIS5 stage, have infinite radiocarbon dates and originate from the Beringian territory (Fig. 14B). Among them are the already mentioned above remains from Bolshoy Lyakhovskiy Island.

The lack of evidence for the presence of the species outside Beringia can be explained in two ways: either the amount of material found and studied is insufficient, or there is evidence of a real range break due to the reforestation of eastern Siberia during the Last Interglacial, similar to what happened in the Holocene. In MIS4 (there is very little data) and MIS3, a range break between Beringia and the area south of the Verkhoyansk Ridge cannot be excluded either (Fig. 14C).

Of particular note is the recent unique discovery of lion remains on the Gydan Peninsula (Lake Yambuto, 71°N, Fig. 14C) as part of the mammoth fauna typical of the Arctic regions of Eurasia (Kosintsev and Gimranov, 2018). The dates on mammoth, horse, bison and reindeer

bones range from 36877±1466 cal years BP (SPb –3023) to 22667 ±195 cal years BP (SPb-3032), and most of them correspond to the MIS3 stage. It is therefore likely that the cave lion entered this part of northern Asia during relatively warm interval (Karga = Bryansk = Denekamp interstadial) of the MIS3 stage.

For the MIS2 stage, seven dates derived from cave lion remains ranged from 26843 to 14621 years BP. The confidence interval for the youngest date (Barnett et al., 2009) from the Lena River Basin was 14971–14285 cal years BP (OxA-12901) (Bølling oscillation, GI-1e). A slightly earlier date with the confidence interval of 15106–14444 cal years BP (OxA-13833) was obtained on specimen from the Arga-Yurekh River Basin [Barnett et al., 2009] (Fig. 14D). To this list, we add one indirect (wood) date from the Dyuktai Cave deposit (Aldan River basin) of 14019±208 cal years BP (LE-907) (Mochanov, 1970).

Thus, the available data allow us to consider the hypothesis of the extinction of cave lions in East and Northeast Asia because of the gradual decline of populations both in Beringia and in other parts of the region, at the latest at the boundary between the Bølling warm oscillation (GI-1e) and the Dryas II cooling (Older Dryas, GI-1d).

3.13. Region 11 – North America

The range of the Beringian cave lion (*P. spelaea vereshchagini*) in North America was restricted to the Alaska territory (Fig. 15). The only

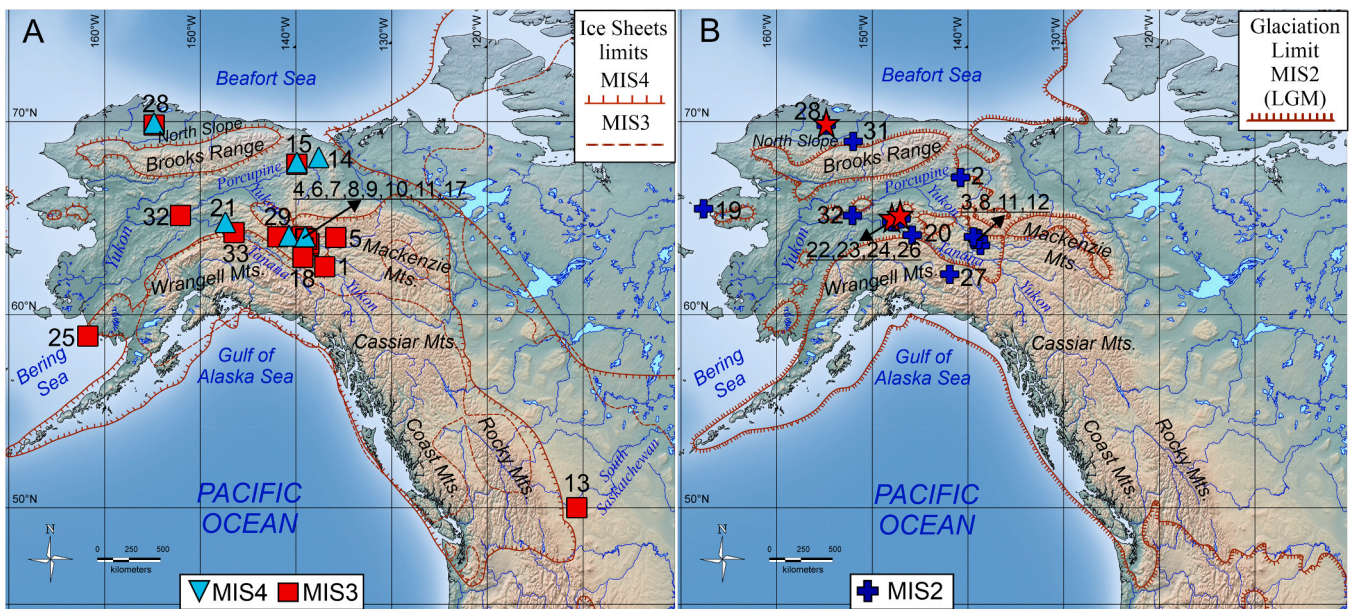


Fig. 15. The sites with cave lion remains in the Region 10 – North America; the sites with the youngest cave lion remains dated directly (red asterisks) are marked: 1 – Big Creek, 2 – Bluefish Caves, 3 – Dominion Creek, Loc. 49, 4 – Dominion Creek, Loc. 50, 5 – Dublin Gulch, 6 – Gold Run Creek (Dawson Loc. 32), 7 – Gold Run Creek (Dawson Loc. 33), 8 – Hunker Creek, 9 – Hunker Creek (Dawson Loc. 10), 10 – Hunker Creek (Dawson Loc. 12), 11 – Hunker Creek (Dawson Loc. 16), 12 – Hunker Creek, Dawson (1978), 13 – Medicine Hat, 14 – Old Crow Basin, 15 – Old Crow River, Loc. 11 A, 16 – Quartz Creek, 17 – Sixtymile Area River, Loc. 3, 18 – Thistle Creek, 19 – Banner Creek, 20 – Big Delta D-6, 21 – Cripple Creek, 22 – Ester Creek, 23 – Fairbanks area, 24 – Fairbanks Creek, 25 – Fox Gulch, 26 – Gold Hill, 27 – Gold Run Creek, 28 – Ikpikpuk and Titaluk Rivers, 29 – Lost Chicken Creek, 30 – Lower Gold Sream, 31 – North Slope, 32 – Tanana River, 33 – Canyon Creek, Tanana River.

record indicating a southward migration of the animals is the remains dated to the first half of MIS3 from the Medicine Hat site in the South Saskatchewan River Basin (Alberta, Canada), which is located at 50°2'15''N (Reynolds et al., 2019). In our opinion, both direct and indirect evidence for the presence of this species in eastern Beringia is still lacking, at least until MIS4. This limits the content of hypotheses about the timing of lion migration(-s) from western Beringia.

The oldest finite date for cave lion remains in the region is 51405 ± 2043 cal years BP (CAMS-91784) from the "Ikpikpuk and Titaluk Rivers" site, which is located at ~69°51'23''N. The youngest date that was obtained from the same site has a confidence interval of 13298–13099 cal years BP (CAMS-53909) (Mann et al., 2015). The species probably became extinct in eastern Beringia during the Allerød warming (GI-1c-a).

4. Discussion

The list of extreme "points" of the cave lion's range in Middle – Late Pleistocene of Eurasia and North America is as follows. The southern limit of the cave lion's range is marked by its Middle Pleistocene remains from the Bear's Cave (Israel) (Tchernov and Tsoukala, 1997) that located at 32°56'14.2''N. For finds from the Middle East, confirmation that they belong to the cave lion through ancient DNA is highly desirable, as this area falls within the range of the African lion. The northernmost finds of Late Pleistocene lions (probably the Last Interglacial, MIS5e) are known from Bolshoi Lyakhovskiy Island (Novosibirsk Islands Archipelago, Russia), at ~73°19'53.8''N latitude (Barnett et al., 2009; Stuart and Lister, 2011). At least in the Late Pleistocene from the west, the range of the cave lion was restricted to areas in the south-west of the Iberian Peninsula. Lion remains are known from the Gruta de Salemas and Figueira Brava caves (Portugal) located at 9°12'6.00''W and 9°5'59.9''W respectively (Zilhão, 1995; Cardoso, 1996b).

In Northeast Asia, the most easterly find came from the Maly Anyuy River basin at longitude 161°26'24''E – 165°7'18.85''E (Baryshnikov and Boeskorov, 2001; Kirillova et al., 2015). There is an opinion that the

lion was encountered further east, throughout Chukotka region (Vereshchagin, 1971). However, no evidence of its presence, or that of other megafauna species (Puzachenko et al., 2021), has been found. To the east of the Maly Anui basin and up to the Chukchi Peninsula, there is a mountainous area with maximum altitudes of up to ~1700–1890 m. This area is characterised by a number of mountain ranges and plateaus, including the Anyuisky Ridge, Rauchuan Ridge, Pegtymel Ridge Anadyr Plateau, and others. The mountain ranges are situated in latitudinal-meridional direction, overlapping potential routes of animal movements. During the cold periods of the Pleistocene, mountain glaciation was widespread in this area. It is probable that the ecological conditions of the northeastern edge of Asia were unfavourable for both predators and their prey.

In North America during the Late Pleistocene, the northern limit of the range followed the Ikpikpuk and Titaluk rivers basins at approximately 69°51'23.25''N (Mann et al., 2015). The westerly find of lion remains was from the Banner Creek basin (Stuart and Lister, 2011) at ~167°37'44.39''W.

The data on cave lion remains presented above allow us to formulate hypotheses about the processes of early dispersal and extinction of representatives of this evolutionary lineage. A number of uncertainties, usually inherent in palaeontological data, limit the "plausibility" of these reconstructions.

Fig. 16A shows two sets of sites dated to the MIS30–MIS20 (EP) and MIS19–MIS12 (MP-I) intervals. Firstly, it should be emphasised that so far no Early Pleistocene cave lion remains were found in the region of the Middle East, which is considered the potentially primary "source" of the migration into Eurasia. Secondly, it should be noted that by the interval ~MIS30–MIS19 (1.1–0.76 Ma BP), cave lions had apparently already colonised northern Eurasia, from Britain to northeast Asia.

Further, we cautiously suggest that there were two main migration routes to the west in Europe. The "southern" rout was along the north of the Balkan Peninsula, south of the Alps and "northern" route was along the northern slope of the Carpathians, further north-west along the Sudetes and westwards along the watershed of the modern Rhine River and the

Weser, Ems (= Eems) rivers.

Cave lions arrived into Britain more likely around 0.84–0.79 Ma (MIS20), i.e. during the glacial, against a background of falling global sea level. The species may penetrated in the northern part of the Apennine Peninsula in the Early Pleistocene (MIS20), but occupied it most likely during the Middle Pleistocene only (MIS18–MIS15). The expansion into south-southwestern Europe probably occurred in the mid-Middle Pleistocene, in MIS13–MIS12 (~0.5–0.4 Ma). At about the

same time, the cave lion reached the southern Balkan Peninsula.

A very early find of a cave lion in southern Siberia (MIS30–MIS28) (Sotnikova and Foronova, 2014) seems to indicate that the first direction of migration was eastwards. This event roughly corresponds to the Jaramillo subchron (Herrero-Bervera and Thayer, 1986) and the "Mid-Pleistocene Transition" (Maslin and Ridgwell, 2005). Unfortunately, no traces of this movement found. Therefore, the path shown by the dotted line in Fig. 16A is purely hypothetical. The "southern variant"

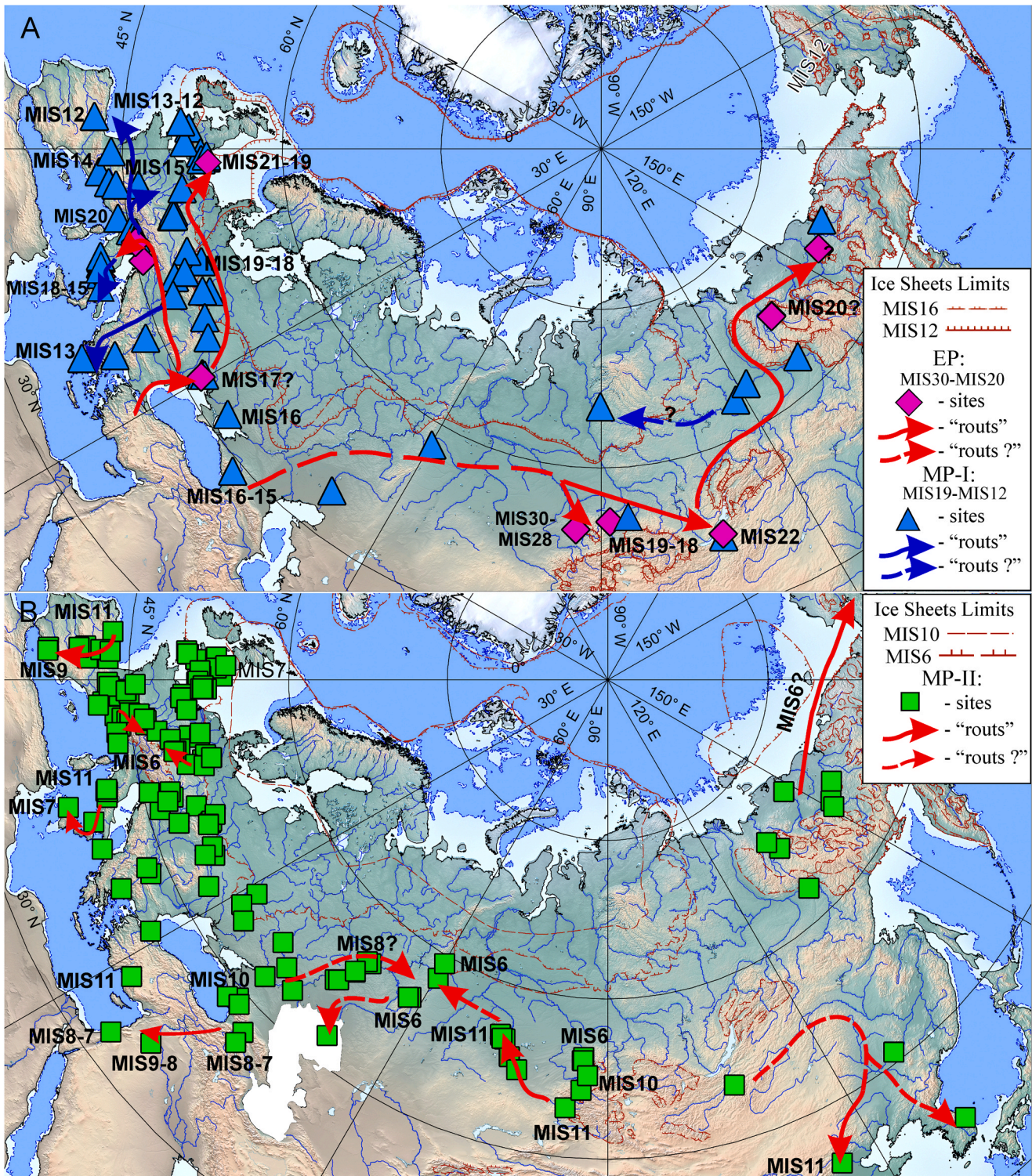


Fig. 16. Sites with cave lion remains dated to time windows EP, MP-I (A) and MP-II (B) with putative migration routes. Fig. 16 (continued). Sites with cave lion remains dated MIS5–MIS4 (C) and MIS3 (D) with putative migration routes.

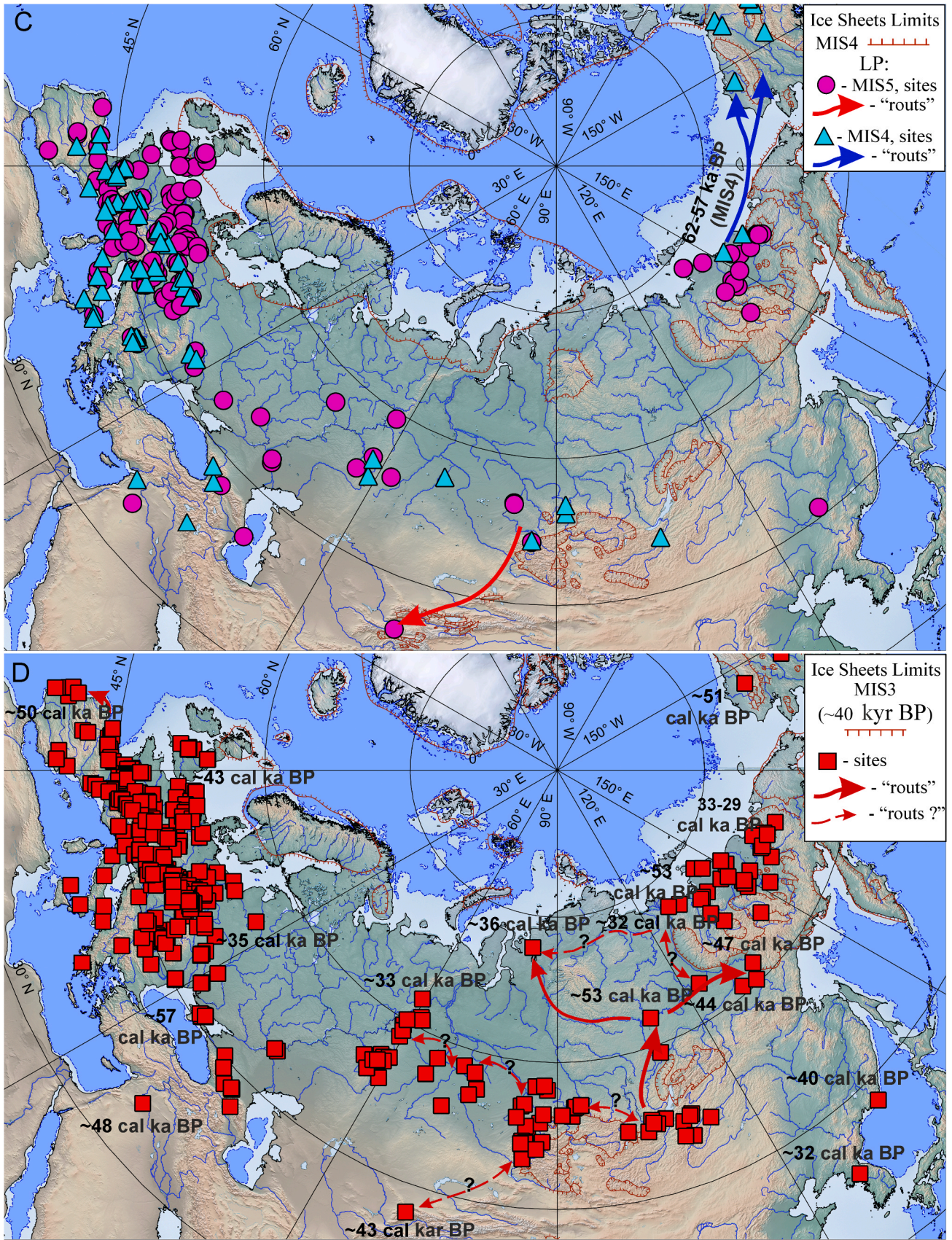


Fig. 16. (continued).

– along the mountains of southern Central Asia – can be considered as an alternative. The time interval between MIS30 and MIS19 was early cave lion dispersion in Asia. In Transbaikalia, lion remains were dated to MIS22 stage. Somewhat later (MIS20–MIS19), the animals reached north-eastern edge of Asia. We believe that the migration route was along the Lena River Basin, west of the Verkhoyansk Ridge. There was also an expansion of the range of cave lions in Asia during the MP-I window, but it is poorly dated.

During the late Middle Pleistocene, regional range shifts occurred in Europe. Among other things, cave lions migrated to the south of the Iberian Peninsula and penetrated into Sicily (Fig. 16B). A "reverse" migration of cave lions to the Near East probably occurred at this time (Elsuède and Savioz, 2017). Regional range shifts also occurred in Asia. We suggest that lions entered the Far East region along the Amur River basin and further south along the Great Khingan Range (Fig. 16B). It cannot be excluded that the lion population was isolated from the rest of its range at the end of the Middle Pleistocene in northeast Asia.

At the beginning of the Late Pleistocene, there were no significant changes in the Eurasian range of the cave lion during the MIS5 interglacial (Fig. 16C). We note the migration of animals into southern Central Asia that occurred at this time. An isolated (?) population of *P. s. vereshchagini* existed in northeastern Asia during this interglacial.

During the first phase of the Last Glacial (MIS4) in Europe, the northern limit of the species range shifted southwards.

During the period of climatic warming in the MIS3 stage, the range of the cave lion expanded in Western and Central Europe and in the western part of Eastern Europe. At the same time, the species has not been found in the vast area between the Dnieper basin and the Urals (Fig. 16D).

In Asia, we do not rule out a northward migration of the lion from southern Siberia (Baikal region). A likely migration route could be the Lower Tunguska River Basin and further along the Yenisei River Basin, leading to the appearance of animals on the Gydan Peninsula (Fig. 16D).

However, another possible migration route is from the east, directly from the range of the Beringia subspecies through the North Siberian Lowlands. We cannot rule out the possibility that South Siberian lions have crossed into western Beringia. This could have led to genetic exchange with *P. s. vereshchagini*. Future palaeogenetic studies may be of great help in resolving these issues.

In Western Siberia, a spatial grouping in the Irtysh River basin was apparently represented in MIS3. We do not exclude the possibility of exchange between this grouping and populations in the Urals and the upper Ob' River basin. A.V. Shpanskiy and S.V. Svyatko (Shpanskiy and Svyatko, 2018) suggested that the extinction of lions in western Siberia occurred earlier than in other parts of their range. Indeed, there are no dates for cave lion remains, which corresponded to time not only to the LGM, but also to the end of the MIS3 stage. When interpreting the data from Western Siberia, it should be borne in mind that they are derived from alluvial deposits and are practically unknown from watersheds. Given the nature of the sediments, more direct dating is required. So far, it is quite likely that the cave lion became extinct in MIS3, at least in the Irtysh River Basin.

The end of the Pleistocene is a period of gradual extinction of the cave lion. This process was in general described previously (Stuart and Lister, 2011). Based on the available data, the extinction of species throughout the Eurasian range did not occur at "one time" (Fig. 17). The distribution of dates probably indicates several "waves" of extinction. The earliest can be correlated with the second half of MIS3 and possibly the very beginning of MIS2. Apart from the plains of western Siberia, this wave affected the Far East, the British Isles, northern Europe and some other regions. The beginning of the next extinction "wave" correlates with the end of the LGM, namely the Greenland Stadial GS-2.1. This is followed by the Oldest Dryas (GS-2a) and the Bølling warming (GI-1e) when the extinction spreads over virtually the entire species range, from the Pyrenees to northeast Asia (green triangle in Fig. 17).

The extinction of lions in western Beringia probably occurred no

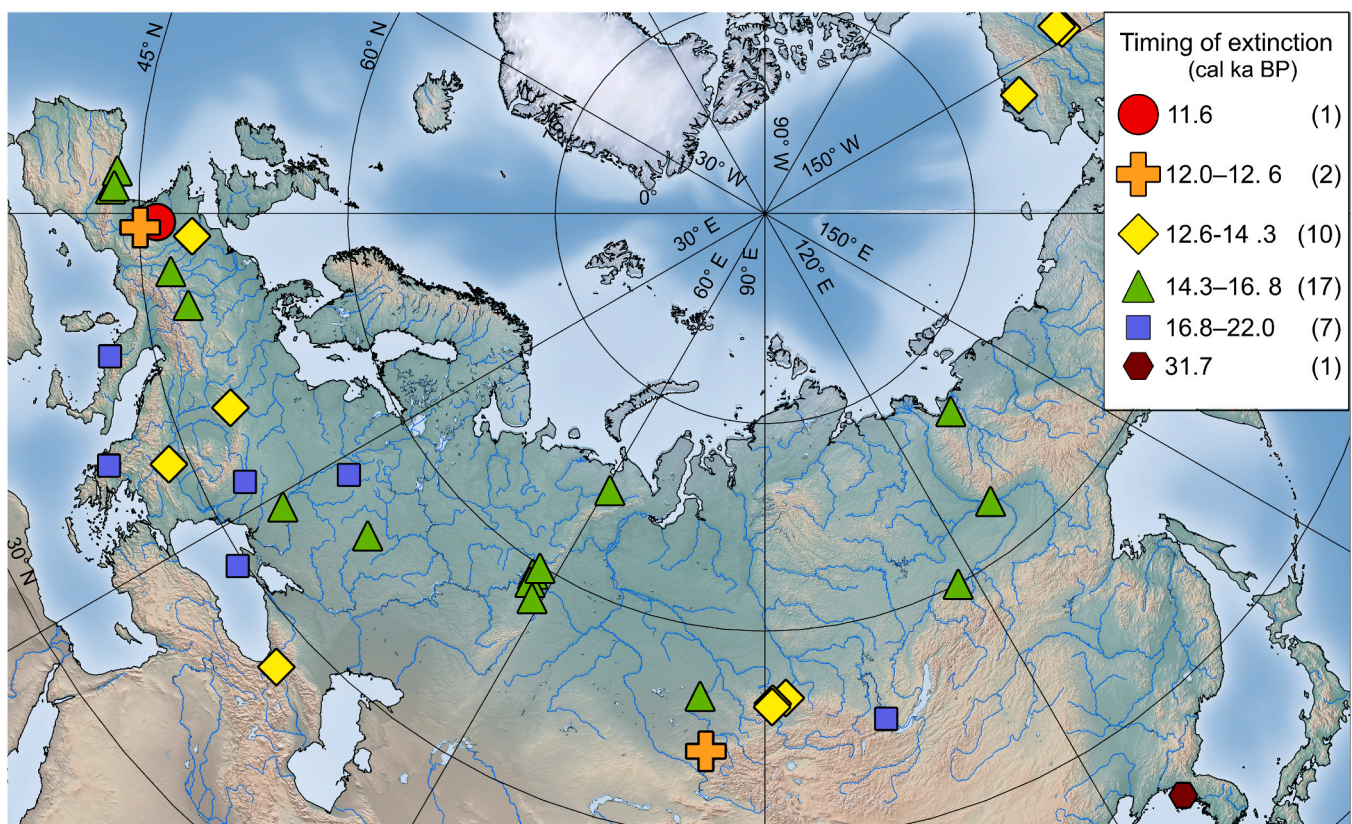


Fig. 17. The "timing" of the cave lion extinction.

later than the GI-1e interstadial (Bølling), while in eastern Beringia, Alaska, they became extinct some later, but before the Younger Dryas (GS-1). Changes in regional climate during this period led to significant transforming of vegetation cover and overall landscape structure. The gradual transition from highly productive Pleistocene arctic and sub-arctic steppe to less productive wet tundra had a negative impact not only on woolly mammoth (Pitulko and Nikolskiy, 2012) and woolly rhinoceros (Puzachenko et al., 2021) populations, but also on the smaller herbivorous ungulates that formed the basis of the cave lion's diet, and consequently on the cave lion itself. The next stage of the reconstructed extinction in Eurasia occurred from the Older Dryas cooling to the Allerød warming (GI-1d-a) (yellow diamonds in Fig. 17). Finally, the few remaining regional groups of cave lions disappeared during the GS1 that corresponding to the Younger Dryas cooling. In a few exceptional cases (Europe), the cave lion may have persisted locally into the early Holocene.

We identified two features of the cave lion range decline in the Late Pleistocene in Eurasia: 1) the most recent populations are somehow usually associated with foothills in mountainous regions (Figs. 17, and 2) there is no obvious link between the extinction and "density" of human settlement of the area. At the end of the Pleistocene, the area of Europe within the lion's range was the most populated, but it was in Western Europe that the lion was reported to have persisted the longest. A similar pattern is known to exist in the case of European bison (wisent) (*Bison bonasus* (L., 1758)), auroch (*Bos primigenius* Bojanus, 1825) or tarpan (*Equus ferus ferus* Boddaert, 1785). In our opinion, the primary cause of the extinction of cave lion as the indicator of the late "mammoth fauna" in Eurasia at the end of the Pleistocene was the qualitative and irreversible reduction of its food base. The radical reduction in the density of ungulates (mainly reindeer, cabaloid and non-cabaloid horses, steppe bison) and the changes in their ranges led to the undermining of the traditional food base of the cave lions, which could only survive in conditions of high abundance of potential prey (as was the case in the African savannah until recently). The persistence of the last populations in the foothills was probably due to the persistence of the most likely reindeer population in these areas and the persistence of hunting opportunities in open, unforested areas. The shift of the southern limit of the range northwards in Eastern Europe during the Late Glacial time and the discovery of lion remains in the Subpolar Urals in GS-2a may reflect the northward movement of lions following their main prey – herds of ungulates. It is possible that humans (*Homo sapiens* L., 1758) in Europe hunted cave lions during the Late Pleistocene period. However, it is unlikely that anthropogenic factors played a decisive role in the extinction of the species. The long history of coexistence of humans and lions in Africa (before the period of firearms use) provides indirect evidence in favour of our hypothesis.

The most significant Middle Pleistocene migration occurred in eastern Asia, when the ancestors of *P. atrox* (Leidy, 1853) crossed the shelf, most likely north of Chukotka, to the New World (Fig. 16A). During the Middle and Late Pleistocene, a chronopopulation of cave lions existed in the area of western Beringia, which at various times was the source of emigration to North America. The available palaeontological evidence seems to support the hypothesis of gradual evolution in Beringia. The lion was well adapted to the climatic conditions of the region due to its long stay in the far north of Eurasia, including north of the Arctic Circle. Because of the excellent preservation of the remains buried in the permafrost, we have a great deal of information about the biology of this geographic grouping of lions. The Beringia cave lion had a number of peculiarities: 1) relatively small size (in some cases the smallest of the species), 2) strongly expressed sexual dimorphism in canine size with relatively weak sexual dimorphism in overall size, 3) the most flattened from the sides predatory tooth m1, which could better perform the cutting function when dismembering prey, and its complete utilisation, important when living in the harsh conditions, especially in winter (Kirillova et al., 2018; Boeskorov and Baryshnikov, 2013; Puzachenko and Baryshnikov, 2024). Studies of the coat of the Beringia lion

have shown that it contains a dense, high-fuzzy undercoat of spiral, thick hairs containing air cavities (Chernova et al., 2020). This undercoat covered the cubs' bodies quite evenly and undoubtedly prevented hypothermia. Other adaptations include the accelerated development of the dental system (compared to the modern African lion), which also increased the cubs' chances of survival (Boeskorov et al., 2021).

The continuity between the "first" lions that inhabited Beringia in the Middle Pleistocene and the Late Pleistocene *P. s. vereshchagini* is still uncertain. In recent study (Stanton et al., 2020), two deeply diverged mitogenome clades in the cave lion were identified. One of these clades was restricted to Beringia (matched to *P. s. vereshchagini*) while the other was prevalent across western Eurasia (matched to *P. s. spelaea*) and the estimated time of divergence for these clades was about 578 ka BP (~MIS 15). It is more likely that the ancestor of *P. s. vereshchagini* was the source of first wave of lion migration to North America. Barnett et al (Barnett et al., 2009). found evidence of genetic divergence between *P. s. vereshchagini* and the American lion (*P. atrox*) within the 95 % interval of 489–194 ka BP (MIS13–MIS6), and a most recent common ancestor of *P. atrox* lived in the interval 346–118 ka BP (MIS10–MIS5).

The possibility of lion migration from Asia to North America has existed since the early Middle Pleistocene, at least since the appearance of the species in Western Beringia. Therefore, the very possibility of such migrations (invasions) cannot be excluded. Given the large size of the American lion, its ancestors were likely to have been larger animals in comparison with members of the Late Pleistocene subspecies of the Beringian lion. Although data are scarce, it is reasonable to assume that the cave lions that inhabited Beringia in the Middle Pleistocene were larger than their Late Pleistocene descendants (Baryshnikov and Boeskorov, 2001; Boeskorov and Baryshnikov, 2013). A combination of palaeogenetic data (Barnett et al., 2009) and global climate dynamics (Lisiecki and Raymo, 2005; Batchelor et al., 2019) suggests that successful migration may have occurred during one of the glaciations, when the area of the dried shelf was at its greatest and the "route" from Eastern Beringia to the south, deep into the North American continent, was clear.

To date, no reliable finds of *P. atrox* older than MIS6 have been identified. The local fauna of Tule Springs (site B2, Nevada, USA) includes the remains of a lion and the broad-headed bison, *Bison latifrons* Harlan, 1825. The age of this assemblage has been estimated at ~190–118 ka, based on the species composition (Haynes, 1967; Mawby, 1967). The presence of lion remains indicated at Cumberland Bone Cave (Allegany County, Maryland, USA), with the cave sediments dated to the Cudahy (Lava Creek B) ash at ~0.64 Ma (MIS16) (Gidley and Gazin, 1938; Van der Meulen, 1978). However, we did not find any later confirmation of this early finding of *P. atrox*. The report of an even earlier presence of *P. atrox* (Cedazo locality, Mexico) (Mooser and Dalquest, 1975) with a date in the range of 1.7–1.2 Ma is more likely an error in dating, given that this faunal assemblage also contains *Aenocyon dirus* (Leidy, 1858) and *Bison antiquus* Leidy, 1852.

In relation to the aforementioned issue of the migration of *P. atrox* ancestors, it can be posited that bison firstly migrated to North America during the Late Middle Pleistocene (Late Illinoian) namely in the MIS6 stage (Froese et al., 2017). As a first approximation, it is natural to link both events – the first migration of cave lions and bison from western Beringia to North America – and date them to the MIS6 stage. We expect that future palaeogenetic studies will allow us to significantly reduce the time interval for the divergence of *P. spelaea* and *P. atrox*, and that new discoveries and dating of lion remains from North America will allow clarifying the chronology of the event. It is probably necessary to consider the migration of lions and bison in the late Middle Pleistocene not as separate independent events, but as part of a migration wave from northeast Asia (one of a series of several that occurred in the Pleistocene) that also picked up other species (*Vulpes vulpes* (L., 1758), *Canis lupus* L., 1758, *Alces americanus* (Clinton, 1822), *Cervalces* sp. Scott, 1855, *Rangifer tarandus* (L., 1758), *Ovibos moschatus* (Zimmermann, 1780),

Mammuthus primigenius (Blumenbach, 1799) and others). The second bison invasion dates back to MIS3 and MIS2 stages (Mooser and Dalquest, 1975), i.e., somewhat possibly later than the second wave of lion migration, which occurred not earlier than the end of the Sangamonian Interglacial (MIS5). The cave lions inhabiting eastern Beringia in the second half of the Late Pleistocene (MIS4–MIS2) were descendants of *P. s. vereshchagini* emigrants from western Beringia (Stanton et al., 2020). It is thought that the second (last?) migration wave of cave lions to North America most probably took place during the MIS4 stage only.

The evolutionary history of the cave lion lineage *sensu stricto* probably began in the early Pleistocene. In Eurasia, however, the oldest remains of the cave lion proper (*P. s. fossilis*) are dated to MIS30–MIS28 (Sotnikova and Foronova, 2014). The interval between MIS30 and MIS19, the stage of early cave lion dispersal in Eurasia, is referred to in this study as the EP time window. The next MP-I time window covers the first half of the Middle Pleistocene between MIS19 and MIS12. The MP-II time window covers the late Middle Pleistocene between MIS11 and MIS6. Presumably, some morphological change occurred in MP-II that led to the formation of the Late Pleistocene cave lion "morphotype", at least in some parts of the range (Argant and Brugal, 2017; Boeskorov and Baryshnikov, 2013). At the end of the Middle Pleistocene, an early chronotaxa *P. s. fossilis* was replaced by the smaller *P. s. spelaea*. The intermediate chronotaxa, *P. s. intermedia* was described from the end of the Middle Pleistocene in Europe (Argant and Brugal, 2017).

In recent decades, the results of palaeogenetic studies added to the traditional arsenal of palaeontological methods. There are many examples of the productivity of this approach. According to the scheme based on metagenomics data, the genus *Panthera* diverged from sister genus *Neofelis* or Pantherini including *Neofelis* diverged from Felini lineage (Zhang et al., 2023) around 10.0 Ma (14 – 5.95 Ma) (Barnett et al., 2016; Tseng et al., 2014). Both genera, *Panthera* and *Neofelis*, including archaic species *P. tigris* (L., 1758), were distributed in Southern Asia or/and South–Eastern Asia, which can be regarded as the place of origin for panther-like felids (Hemmer, 2023). Then, at about 4.6 Ma pantherines penetrated into East Africa, where they formed several taxa, including sister species *P. pardus* (L., 1758) and *P. leo*, which diverged about 3.7 (3.2) Ma (Hassanin et al., 2021; Werdelin et al., 2010; Figueiró et al., 2017). The time of divergence of *P. spelaea* and *P. leo* was estimated by the molecular clock to be 1.7 (1.5) Ma (Hassanin et al., 2021). The cave lion lineage began to colonise Eurasia at the end of the Early Pleistocene, but no later than the beginning of the Middle Pleistocene (~1 Ma), when the species *P. spelaea* emerged. The origin of the ancestors of the cave lion is usually associated with Africa, which is not surprising given the obvious morphological and genetic similarities between the cave lion and the African lion. However, hypotheses linking the origin of the cave lion to an Asian (South Siberian) lion-like pantherine lineage that is closely related to the *P. leo* lineage are also possible. This hypothesis would "explain" the lack of palaeontological evidence for the migration of cave lions from Africa to Asia at the end of the Early Pleistocene.

Some principal aspects in the cave lion evolution, highlighted based on palaeontological data, at least do not contradict the results of genetic studies (Barnett et al., 2009; Stanton et al., 2020). Nevertheless, molecular phylogenetic constructions, particularly those based on mitogenomic data, should be treated with a degree of caution (Ho et al., 2015; Bannikova and Lebedev, 2022). There is no single "true" model for the "molecular clock", and these "clocks" in different phylogenetic lineages may run at different, usually unknown, rates (Ho et al., 2015). Molecular clocks are calibrated using palaeontological data, for which the range of dates can be millions of years (see, for example, (Hassanin et al., 2021)). Palaeontologists and biologists studying modern species then often use the results of molecular genetic studies uncritically, interpreting the calibration results as if they were independent estimates of divergence times derived solely from the degree of genetic similarity/difference between taxa. C. Broggin et al (Broggin et al., 2024). published the results of genetic studies that significantly contradict the model of cave

lion evolution presented above. The main contradiction is caused by the inconsistency of mitogenomic and microsatellite estimates of the time of divergence of cave and African lion lineages with previous genetic studies and, more importantly, with data from the palaeontological record. The authors conclude that emigration from Africa and subsequent divergence within the cave lion lineage occurred only about 175,000 years ago (MIS6). We suggest that this result is due to incorrect calibration of the molecular clock. In general, the relatively low level of divergence of genetic markers (*cytb*, nuclear microsatellites) is more indicative of their conservatism and relatively low rate of evolution.

5. Conclusion

The palaeontological material accumulated over the last 50 years even allows us to present in this study the modern view of the distribution of cave lions in Eurasia and North America during the Middle - Late Pleistocene. Our aim was not only to provide a more complete description of the range on a continental scale, but also to provide a more detailed picture of the species' dispersal and to place the relevant events in a chronological context. However, this does not mean that the history of cave lions is now fully understood and reconstructed. There is still competition between different hypotheses. Although the probability of obtaining new data that would significantly alter our current ideas is relatively low, it is not zero.

In this study, we have not considered in detail different chronosubspecies or chronospecies of cave lions and geographical evolution according to different palaeoenvironments and climatic variations (role of glaciated areas) in the second half of the Pleistocene.

The range of radiocarbon dates already available from cave lion remains will allow future studies of population dynamics in certain parts of their range at the end of the Late Pleistocene.

Finally, a number of biological characteristics of cave lions require further investigation. This list may include the study of adaptation to both cold and relatively hot climates, the peculiarities of the dietary spectrum in different parts of the range, on plains and in mountainous areas, analyses of possible spatial and other relationships with potential prey, including testing the hypothesis of seasonal migration of animals, etc. It is also of great importance to examine the relationships between the cave lion and other large carnivores and potential competitors, including the cave hyena and cave bear in Europe and Asia (Diedrich, 2011), as well as the short-faced bear (*Arctodus simus* Cope, 1897) in America.

There is no doubt that the palaeogenetic database of nuclear and mitochondrial DNA should be significantly expanded, both qualitatively and quantitatively, to better understand the evolution of the species and the history of its range.

Our study, as well as other publications in this volume, summarises the results of a certain stage of cave lion research, and we hope that it will provide the necessary basis for further work on cave lions – this remarkable representative of Pleistocene megafauna.

Finally, we would like to emphasise the crucial role of large-scale international free collaboration in the pooling of data for this study. Comprehensive studies of the evolutionary history of wide-ranging taxa such as the cave lion are only possible through the combined efforts of specialists from different countries.

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Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Martin Sabol reports financial support was provided by Slovak Research and Development Agency. Martin Sabol reports was provided by Slovak Scientific Grant Agency. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

All data used for the study are contained in the attached Supplementary-Material-DataBase

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.hisbio.2024.100006](https://doi.org/10.1016/j.hisbio.2024.100006).

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