



# The Quaternary lions of Ukraine and a trend of decreasing size in *Panthera spelaea*

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## Abstract

The fossil record of the cave lion, *Panthera spelaea*, suggests a gradual decrease in body size, the process peaking just before the extinction of the species at the end of the Late Pleistocene. Such an evolutionary trend appears rather unusual for a large felid species and requires further investigation. This study reviews the cave lions of Ukraine, whose fossils are known from 46 localities dated from 800 kyr to 18–17 kyr ago, with a special emphasis on size changes through time. We describe several important finds including those of *Panthera spelaea fossilis* from Sambir, *Panthera spelaea ssp.* from Bilykh Stin Cave and *Panthera spelaea spelaea* from Kryshtaleva Cave. We make subspecific identifications of specimens from the region and focus on their size characteristics. Our analysis of Ukrainian cave lions agrees with the temporal trend of decreasing size, particularly accelerating during MIS 2, as exemplified by the extremely small female skull from Kryshtaleva Cave. We provide a direct AMS date for this specimen (22.0–21.5 cal kyr BP), which suggests that the Kryshtaleva lioness must have belonged to a *Panthera spelaea spelaea* population forced south by the spreading ice sheet. We discuss some palaeoecological aspects of the evolutionary history and eventual extinction of the cave lion. Finally, we review the subfossil records of the extant lion *Panthera leo* known from several Ukrainian sites archaeologically dated to 6.4–2.0 kyr BP. These finds most probably represent the Persian lion *Panthera leo persica*.

**Keywords** Carnivora · Felidae · Skull · Body size · Pleistocene · Holocene

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## Introduction

When thinking about the cave lion *Panthera spelaea* (Goldfuss, 1810), an image of a huge, massive and maneless animal comes to mind. Partially this is true since the first lions that entered Eurasia were among the largest felids that ever existed (Kurtén 1960, 1968; Dietrich 1968; Hemmer and Schütt 1970; Argant 1988, 1991, 2000; Hemmer 2003, 2004; Sotnikova and Nikolskiy 2006; Argant et al. 2007; Barycka 2008; Sabol 2014; Sotnikova and Foronova 2014; Argant and Argant 2018; Marciszak et al. 2019, 2020a). Recent studies support the species status of *P. spelaea* separate from the extant lion *Panthera leo* (Linnaeus, 1758) (Argant 1988, 1991; Barnett et al. 2009, 2016; Marciszak et al. 2014, 2019, 2020a, b; Ersmark et al. 2015; Argant and Brugal 2017; de Manuel et al. 2020). The cave lion species was not monotypic and included three chronologically successive subspecies. The oldest, largest and longest-existed was *Panthera spelaea fossilis* (von Reichenau, 1906) whose presence is documented in at least 62 Eurasian sites dated between 1200 and 300 kyr BP (David 1980, 1999; Sala 1990; Lewis et al. 2010; Hemmer 2011; Sotnikova and Foronova 2014; Marciszak et al. 2019, 2020a; Prat-Vericat et al. 2022). The second subspecies, on average smaller and less massive, *P. s. intermedia* Argant et Brugal, 2017, has been erected based on the material from Igue-des-Rameaux (France, 300–250 kyr BP; Argant and Brugal 2017; Brugal et al. 2020; Persico 2021); morphologically similar lions with ‘intermediate’ features are known from various European sites dated to 300–180 kyr BP (Hemmer 1974, 2011; Schütt and Hemmer 1978; Argant et al. 2007; Argant 2010; Marciszak and Stefaniak 2010; Marciszak et al. 2014, 2020a, b). The stratigraphically youngest subspecies, *P. s. spelaea* (Goldfuss, 1810), which was also the most diverse metrically and morphologically, appeared 180–160 kyr BP (Marciszak and Stefaniak 2010; Hemmer 2011; Sabol 2011a, b, 2014).

The three subspecies of the cave lion differ in size and several morphological features. As compared to *P. s. fossilis*, *P. s. spelaea* possesses: larger incisors; more flattened and narrower canines; narrower P3 with shorter and higher paracone, more reduced protocone and metastyle and weaker distal cingulum; narrower P4 with shorter protocone, smaller and lower parastyle, and paracone shorter than metastyle; narrower p3 with shorter and lower protoconid; shorter and narrower p4 with longer and lower protoconid; more elongated and narrower m1, which is longer than p4 and has higher and longer protoconid and weaker or absent median lingual bulge (Kurtén 1960; Dietrich 1968; Hemmer and Schütt 1970; Ballezio 1975; Schütt and Hemmer 1978; Argant 1988, 1991; Groiss 1992, 2002; Gužvica 1998; Baryshnikov and Boeskorov 2001; Hemmer 2003, 2004; Bona 2006; Sotnikova and Nikolskiy 2006; Argant et al. 2007; Hankó 2007; Barycka 2008; Baryshnikov and Tsoukala 2010; Bona

and Sardella 2012; Sabol 2014; Sotnikova and Foronova 2014; Marciszak et al. 2014, 2019, 2020a, Prat-Vericat et al. 2022). According to Argant and Brugal (2017), *P. s. intermedia* is smaller than *P. s. fossilis* and has: less massive muscle attachments; a shorter and triangular-shaped mandibular ramus with shallower and shorter masseteric fossa; narrower canines; narrower P4 with almost straight buccal margins; narrower m1 with less developed median bulge; and more gracile metapodials and calcaneus.

Among the most intriguing aspects of the cave lion lineage is an evolutionary trend of decreasing body size. Proposed as a general pattern by some authors (Kurtén 1960, 1968; Dietrich 1968; Schütt 1969; Hemmer and Schütt 1970; Argant 1988, 1991, 2000; Gužvica 1998) and questioned by some others (Lewis et al. 2010), this trend started as early as MIS 6/5 and accelerated during MIS 3 and MIS 2 (Argant et al. 2007; Hankó 2007; Barycka 2008; Sabol 2014; Marciszak et al. 2014, 2019, 2020a, b).

This process is well documented based on Western and Central European fossils of the cave lion, whereas finds from Eastern Europe are less known overall and even less so in terms of size evolution. Ukraine is of special interest in this respect because its vast and mostly flat territory served as an important migratory corridor in an east–west direction. The southern regions of Ukraine alongside the northern coastline of the Black Sea were also important migration pathways between Asia and Southeastern Europe. Numerous finds of Quaternary lions have been reported from this area, but seldom internationally (Fig. 1).

The goal of this study is to review the history of lions in the territory of Ukraine with a special focus on potential changes in their size. We summarise and discuss the available evidence ranging from the early Middle Pleistocene (*P. s. fossilis*) to historical times (*P. l. persica*). We examine several previously undescribed fossils of the cave lion including a surprisingly small skull of *P. s. spelaea* from Kryshtaleva Cave and provide an AMS radiocarbon date for this remarkable specimen. Our analysis reveals the temporal trend of decreasing size in Ukrainian *P. spelaea* and demonstrates that it reached its maximum during MIS 2.

## Material and methods

### Material

The specimens from the following Ukrainian sites were examined:

Bilykh Stin Cave (No. 4 in Fig. 1 and Table 1): right p4 (FCNU-G BS-114); right m1 (FCNU-G BS-129); left radius (FCNU-G BS-123); left metacarpal 2 (FCNU-G BS-120); left metacarpal 3 (FCNU-G BS-113); right talus (FCNU-G BS-54); right capitulum; left metatarsal 4

(FCNU-G BS-119); caudal 5 (FCNU-G BS-25); caudal 7 (FCNU-G BS-82); phalanx 3.

Emine-Bair-Khosar (Bj site) (No. 12 in Fig. 1 and Table 1): body of left mandible without symphysis and with p3-m1 (NMNHU-P Bj-104); metacarpal 2 (NMNHU-P Bj-88); metacarpal 3 (NMNHU-P Bj 83); metacarpal 3 (NMNHU-P Bj 92); metacarpal 4 (NMNHU-P Bj-89); metacarpal 4 (NMNHU-P Bj-93); metacarpal 5 (NMNHU-P Bj-85); metacarpal 5 (NMNHU-P Bj-90); metatarsal 2 (NMNHU-P Bj-84); metatarsal 2 (NMNHU-P Bj-91); metatarsal 4 (NMNHU-P Bj-87); metatarsal 5 (NMNHU-P Bj-86); phalanx 1 (NMNHU-P Bj-94, NMNHU-P Bj-95, NMNHU-P Bj-96, NMNHU-P Bj-97, NMNHU-P Bj-98, NMNHU-P Bj-99, NMNHU-P Bj-100, NMNHU-P Bj-102, NMNHU-P Bj-103); phalanx 2 (NMNHU-P Bj-101).

Kaniv (No. 5 in Fig. 1 and Table 1): left humerus (NMNHU-P 10–789).

Kodak (No. 17 in Fig. 1 and Table 1): left mandibular body with damaged symphysis and worn c1, p4 and worn m1 (NMNHU-P OF-645/3197); fragment of right mandible with p4-m1 (NMNHU-P OF-646/3541).

Kryshtaleva Cave (No. 20 in Fig. 1 and Table 1): intact skull with left I3-P4 and right C1 and P4 (NMNHU-P

OF-803/1964) and mandible with left i2, c1 and p4-m1 and right i3-m1 (NMNHU-P OF-806/1964); left humerus with damaged proximal epiphysis (NMNHU-P OF-805/1964).

Mezhyrich (No. 24 in Fig. 1 and Table 1): left maxilla with C1-M1 alveoli (NMNHU-P 56–916); right maxilla with zygomatic fragment (NMNHU-P 56–917); left scapula (NMNHU-P 56–6660); proximal end of the right humerus (NMNHU-P OF-510/56–4488); distal epiphysis of right humerus (NMNHU-P OF-509/56–1090).

Molodova 1 (No. 25 in Fig. 1 and Table 1): fragments of left maxilla with P3 and worn P4 and right P3 (KIUS MOL 1–84); fragment of left mandibular body with worn m1 (KIUS MI-84); fragment of right mandibular body with p4 and m1 (KIUS MOL 101).

Sambir (No. 2 in Fig. 1 and Table 1): right m1 and right calcaneus (private collection, unnumbered).

Volia-Homuletska (No. 40 in Fig. 1 and Table 1): right p4 and right m1 (private collection, unnumbered).

### Morphometric analysis

The identification of lion specimens was carried out using basic morphometric approaches. Measurements were taken

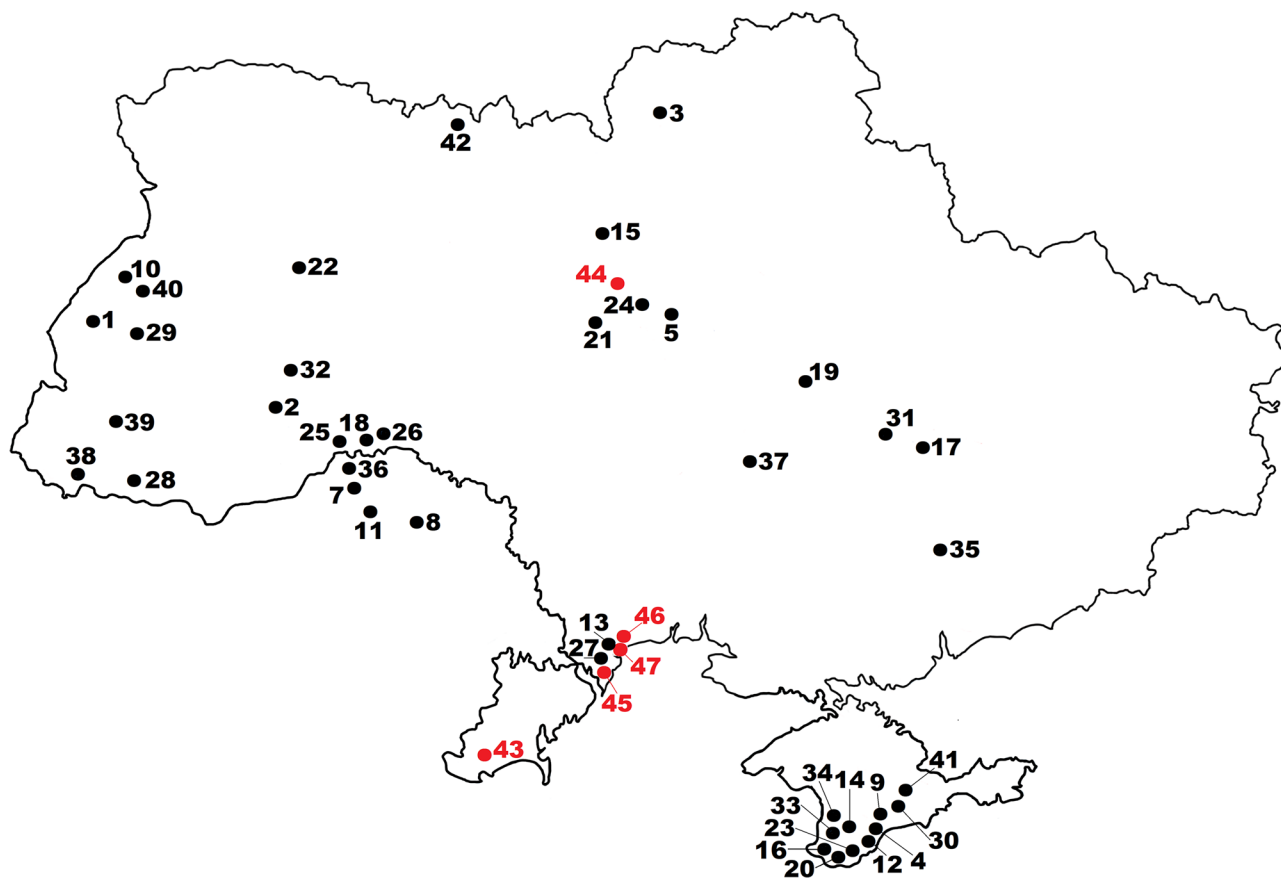


Fig. 1 Records of *Panthera spelaea* and *Panthera leo* in Ukraine and Moldova. The localities are numbered and listed in Table 1

**Table 1** Occurrence of *Panthera spelaea* and *Panthera leo* in the Quaternary of Ukraine, with some adjacent records from Moldova (asterisked). Numbers for localities (Map) correspond to those mapped in Fig. 1

Map	Site	Age (kyr ago)	MNI/NISP	References
<i>Panthera spelaea fossilis</i>				
1	Syniakovo 1	MP (800–700)	11/3	Bachynskyi (1965); Tatarinov (1965); Vereshchagin (1971)
2	Sambir	MP		this paper
<i>Panthera spelaea intermedia?</i> / <i>Panthera spelaea ssp.</i>				
3	Chernihiv	IMP?		Pidoplichko (1956); Tatarinov (1969); Vereshchagin (1971)
4	Bilykh Stin	IMP?	13/1	Ridush (2009, 2010, 2013); this paper
5	Kaniv	IMP/LP	1/1	this paper
<i>Panthera spelaea spelaea</i>				
4	Adzi-Koba	LP (35–28)		Vereshchagin (1971)
7	Brinzeni I*	LP	1/1	David (1980)
8	Buteshty 2*	LP		David (1965, 1980)
9	Buran-Kaya	LP		Tatarinov (1969); Vereshchagin (1971)
9	Chagorak-Koba	LP		Tatarinov (1969)
10	Horodok (Gródek)	LP		Cynkałowski (1961)
11	Duruitore Veche*	LP	18/4	David (1980)
12	Emine-Bair-Khosar, Bj	LP (22–21)	48/1	Ridush and Vremir (2008); this paper
12	Emine-Bair-Khosar, Bc	IMP	3/1	Ridush and Vremir (2008); Ridush et al. (2013, 2018)
13	Illinka	LP (40–27)	6/1	Pidoplichko (1956); Ridush (2009)
14	Kabazi 2	LP (41–30)		Chabai and Uthmeier (2006)
15	Kyiv	LP		Tatarinov (1969)
15	Kyiv-Kyrylivska	LP	1/1	Pidoplichko (1956); Pidoplichko (1938)
16	Kyrylivska Cave	LP		Vereshchagin (1971)
17	Kodak	LP		Pidoplichko (1936, 1969); Korniets (1962); Vereshchagin (1971); this paper
18	Korman' IV	LP	3/1	Tatarinov (1977)
19	Kremenchug	LP	1/1	Pidoplichko (1956); Vereshchagin (1971)
20	Kryshtaleva Cave	LP	53/1	Bachynskyi and Dubliansky (1966); Bachynskyi (1970); this paper
21	Lisovychi	LP	1/1	Pidoplichko (1956)
22	Malaya Ilovysia	LP (40–20)		Bachynskyi (1965); Tatarinov (1965); Ostrovski and Grigoriev (1966)
23	Marmurova Cave	LP	10/1	Ridush and Vremir (2008)
24	Mezhyrich	LP (18–17)	2/1	Haesaerts et al. (2015); Shydlovskiy et al. (2020); this paper
25	Molodova 1	LP (60–45)		Ivanova (1982); Krajcarz and Krajcarz (2012); this paper
25	Molodova 5	LP (60–45)	1/1	Alekseeva (1987); Sotnikova and Foronova (2012)
26	Novodnistrovsk 2	LP (26–25)	1/1	Kulakovska et al. (2020)
27	Nerubaiske	LP		Nordmann (1858); Vereshchagin (1971)
28	Perlyna	LP	11/2	Ridush and Popiuk (2019)
29	Pryima 1	LP	73/5	Matskevychi (2005)
30	Prolom 2	LP		Benecke (1999); Enloe et al. (2000)
31	Romankove	LP		Svistun (1963, 1968); Tatarinov (1969)
32	Rudky	LP		Lubicz-Niezabitowski (1937, 1938); Tatarinov (1969, 2000)
33	Shaitan-Koba	LP		Tatarinov (1969); Vereshchagin (1971)
34	Sjuren 1	LP	1/1	Gromov (1948); Vereshchagin (1971)
34	Sjuren 2	LP (40–25)		Vereshchagin (1971); Benecke (1999)
35	Tykhonivka	LP	1/1	Pidoplichko (1956)
36	Trinka 3*	LP	2/1	David (1980)
37	Volodymyrivka	LP	2/1	Pidoplichko (1956)
38	Vykhvatyntsi	LP	9/2	Zubareva (1949); David (1980); Ketraru et al. (1986)
39	Volyn	LP		Lubicz-Niezabitowski (1925, 1937, 1938)
40	Volia-Homuletska	LP	2/1	this paper
41	Zaskalna 6	LP (60–40)	1/1	Zhuravlev (2016)

Table 1 (continued)

Map	Site	Age (kyr ago)	MNI/NISP	References
42	Zbranky	LP		Tatarinov (1969)
<i>Panthera leo persica</i>				
43	Bolhrad	H (6.4–6.0)	1/1	Bibikova (1973); Vörös (1983)
44	Molukhov Bugor	H (6.0–5.0)		Bibikova (1973)
45	Mayaky	H (5.6–5.3)	9/2	Bibikova (1973); Daróczy-Szabó et al. (2020)
46	Chernovaty	H (2.9–2.5)		Zhuravlev (1981, 1983a, b)
47	Chornomorka 2	H (2.8–2.5)	1/1	Zhuravlev (1981, 1983a, b)
45	Berezan	H (2.7–2.6)	5/1	Zhuravlev (1981, 1983a, 1999); Yanish and Kasparov (2015)
45	Tira	H (2.9–2.0)		Krakhmalnaya (1999)
47	Tyras	H (2.8–2.6)		Daróczy-Szabó et al. (2020)
46	Olviya (Pontic Olbia)	H (2.5–2.0)	10/4	Gromova (1928, 1932); Topachevsky (1956); Zhuravlev (1983a, 1999, 2016)

Abbreviations: *MP* Middle Pleistocene, *IMP* late Middle Pleistocene, *LP* Late Pleistocene, *H* Holocene

with a digital calliper with an accuracy of 0.1 mm. Measuring schemes and morphological terminology (Online Resource 1, Figs. S1, S2, S3, S4, S5, S6, S7, S8 and S9) were chiefly taken from Schmid (1940) and Argant (2010). Measurements of the lion material from Ukraine are presented in Online Resource 1, Tables S1, S2, S3, S4 and S5. Upper teeth are referred to by capital letters (e.g., P4), while the lower ones are given in lowercase (e.g., p4). The MIS (Marine Isotopic Stages) boundaries follow Lisiecki and Raymo (2005). Sexual dimorphism was examined using the canine size (Turner 1984; Van Valkenburgh and Sacco 2002) and m1 size (Gross 1992). Approximate individual age was estimated from dental abrasion (Smuts et al. 1978; Wheeler and Jefferson 2009; Meachen-Samuels and Binder 2010) to ensure the inclusion in morphometric analyses of only adult cranial specimens. Standard estimates of body mass (Online Resource 1, Table S6) were based on the condylobasal length (Van Valkenburgh 1990; Christiansen and Harris 2005) and postcranial elements (Hemmer and Schütt 1970; Hemmer 2001).

In addition to the original measurements, we used the data published by Terzea (1965), Samson and Kovacs (1967), Dietrich (1968), Hemmer and Schütt (1970), Vereshchagin (1971), Altuna (1972, 1981), Hemmer (1974, 2001), Ballesio (1975, 1980), Kurtén and Poulianos (1977, 1981), Schütt and Hemmer (1978), Riedel (1982), Argant (1988, 1991, 2010), Dufour (1989), Groß (1992, 2002), Gross (1992), Turner (1999), Gužvica (1998), Kleczko (1999), García García (2003), Castaños (2005), Bona (2006), Testu (2006), Argant et al. (2007), Hankó (2007), Ovodov and Tarasov (2009), Baryshnikov and Tsoukala (2010), Lewis et al. (2010), Baryshnikov (2011, 2016), Hemmer and Keller (2011), Sabol (2011a, 2014), Sotnikova and Foronova (2014), Argant and Brugal (2017), Pacher (2018) and Sabol et al. (2018).

## Radiocarbon dating

The material from Kryshtaleva Cave was processed at the Department of Human Evolution at Max Planck Institute for Evolutionary Anthropology (MPI-EVA), Leipzig, Germany, using the method described in Talamo and Richards (2011) and Talamo et al. (2021). The outer surface of bone samples is first cleaned by a shot blaster and then 500 mg of bone tissue is taken. The samples are then decalcified in 0.5 M HCl at room temperature until no CO<sub>2</sub> effervescence is observed, usually for about 4 h. 0.1 M NaOH is added for 30 min to remove humics. The NaOH step is followed by a final 0.5 M HCl step for 15 min. The resulting solid is gelatinised after Longin (1971) at pH3 in a heater block at 75 °C for 20 h. The gelatine is then filtered in an Eeze-Filter™ (Elkay Laboratory Products (UK) Ltd.) to remove small (> 80 µm) particles. The gelatine is then ultrafiltered (Brown et al. 1988) with Sartorius “VivaspinTurbo” 30 KDa ultrafilters. Prior to use, the filter is cleaned to remove carbon containing humectants (Talamo et al. 2021). The samples are lyophilised for 48 h. In order to monitor contamination introduced during the pre-treatment stage, a sample from a cave bear bone, kindly provided by D. Döppes (MAMS, Germany), was extracted along with the batch of the archaeological samples (Korlević et al. 2018). To identify the preservation of the collagen yield, C:N ratios, together with isotopic values, must be evaluated. The C:N ratio should be between 2.9 and 3.6, and the collagen yield must be not less than 1% of the weight (van Klinken 1999; Talamo et al. 2021). Stable isotopic analysis was evaluated at MPI-EVA, Leipzig (Lab Code R-EVA), using a ThermoFinnigan Flash EA coupled to a Delta V isotope ratio mass spectrometer. After the evaluation of these values, the samples were sent to Curt Engelhorn Centre for Archaeometry (CEZA), Mannheim, Germany



(Lab Code MAMS), where they were graphitised and dated (Kromer et al. 2013). Calibration was made according to Reimer et al. (2020).

### Abbreviations used in the text

**B**, breadth; **Bd**, distal breadth; **Bm**, mesial breadth; **CBL**, condylobasal length; **FCNU-G**, Department of Physical Geography, Geomorphology and Paleogeography, Yuriy Fedkovych Chernivtsi National University, Chernivtsi; **KIUS**, Archaeological Department, Ivan Krypiakevych Institute of Ukrainian Studies, National Academy of Sciences of Ukraine, Lviv; **L**, length; **M**, mean; **mc**, metacarpal; **MIS**, Marine Isotopic Stage; **mm**, millimetre; **MNI**, minimum number of individuals; **mt**, metatarsal; **N**, number of specimens in the sample; **NISP**, number of identified specimens; **NMNHU-P**, Department of Palaeontology, National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv; **pa**, paracone or paraconid; **pr**, protocone or protoconid; **SD**, standard deviation; **V**, variation.

## Results

### General remarks

Two lion species, *P. spelaea* and *P. leo*, occurred respectively in the Pleistocene and Holocene of Ukraine. The occurrence of *P. spelaea* is known from 46 Ukrainian sites (36 cave localities and 10 open-air sites) dated from the early Middle to the Late Pleistocene (Fig. 1) and covered a time span between MIS 19 and MIS 2 (Table 1). Remains of *P. s. fossilis* were found at two Middle Pleistocene sites, while those of *P. s. spelaea* were documented at 41 localities. Only the record from Syniakovo 1 is dated as late Early or early Middle Pleistocene (Tatarinov 1965; Tatarinov and Bachynskiy 1968; Vereshchagin 1971). The morphology of the Sambir lion corresponds to that of mid-Middle Pleistocene *P. s. fossilis* from Mauer, Mosbach 2 or Château (Marciszak et al. 2019). The material from four sites (Chernihiv, Bilykh Stin Cave, Kaniv and Molodova V) of uncertain age (possibly late Middle Pleistocene), was identified as *P. s. intermedia* or as *P. s. ssp.* The Ukrainian records of *P. spelaea* are dated to the Late Pleistocene or the latest late Middle Pleistocene (MIS 6; Table 1).

Only two AMS radiocarbon dates (60.2 and 56.4 kyr BP, Emine-Bair-Khosar Cave, site Bc) have previously been known for Ukrainian finds of *P. spelaea* (Table 2; Stuart and Lister 2011). These dates are beyond the range of the method and therefore are insufficiently reliable. Herein we report a third date (22.0–21.5 cal kyr BP, Kryshtaleva Cave), which demonstrates that *P.*

*spelaea* survived in Crimea after the Last Glacial Maximum (MAMS-37004 in Table 2).

The material of *P. leo* is known from nine archaeological sites in south-eastern Ukraine dated by archaeological context as 6.4–2.0 kyr BP (Table 1; Bibikova 1973; Vörös 1983; Krakhmalnaya 1999; Zhuravlev 1981, 1983a, b, 1999; Daróczy-Szabó et al. 2020). It is metrically and morphologically similar to the modern Persian lion *P. l. persica*.

Among the material of *P. spelaea*, most of the anatomical parts are represented, with a predominance of fragmentary jaws, isolated teeth, long bones, metapodials, carpals, tarsals and phalanges. Three skulls are known: two almost intact from Chernihiv and Kryshtaleva Cave and one partially preserved from Rudky. Postcranial elements are rare albeit relatively well preserved, even those from open-air sites. All finds of *P. spelaea* are represented by adult individuals, while the material of *P. l. persica* includes juvenile and subadult specimens (Bibikova 1973; Vörös 1983; Zhuravlev 1999).

Apart from Pryima 1 (Matskevych 2005) where 73 bones of at least 5 individuals were collected, the Ukrainian cave lion records are represented by single or few specimens, often found accidentally. The increasing number of these finds during the twentieth century was related to industrialisation and extensive infrastructure development. Information about the exact location and stratigraphical context of such accidental finds is limited or absent. The remains of *P. spelaea* from the Ukrainian open-air sites include those accumulated through natural processes and those deposited in the cultural layer (e.g., Molodova V and Mezhyrich). The material of *P. l. persica* derives from archaeological contexts and more often has cut marks or other signs of human activity (Bibikova 1973; Vörös 1983; Zhuravlev 1999; Daróczy-Szabó et al. 2020). The accumulation of lion remains in caves may be the outcome of natural or catastrophic death, slope or fluvial processes, or activity of carnivorans, e.g., bears (Argant 1988, 1991, 2000; Diedrich 2011a, b, c, d, e, f, 2014, 2017; Sabol et al. 2018; Marciszak et al. 2020b).

Below, we describe the most important specimens of the directly examined material.

### *Panthera spelaea fossilis* (von Reichenau, 1906)

An exceptionally large right calcaneus and a lower carnassial (m1) found in alluvial deposits near Sambir can be reliably assigned to *P. s. fossilis*. According to the calcaneus size (Online Resource 1, Table S5), it exceeds values for *P. s. intermedia* and *P. s. spelaea* and falls into the uppermost range of variation for *P. s. fossilis*. The large size and robustness indicate a big male. Apart from the size, the morphology of the Sambir individual differs slightly from

**Table 2** AMS radiocarbon dates of *Panthera spelaea spelaea* from Ukraine. The  $\delta^{13}\text{C}$  values are reported relative to the vPDB standard and  $\delta^{15}\text{N}$  values are reported relative to the AIR standard for three samples treated at the MPI-EVA. All the  $^{14}\text{C}$  ages are calibrated with 95.4% probability using the IntCal20 atmospheric curve (Reimer et al. 2020) in the OxCal 4.4 software (Bronk Ramsey and Lee 2013)

Site	Bone	Lab code	mg of coll	% coll	$^{15}\text{N}$	%C	%N	$^{14}\text{C}$	cal BP	Source
Emine-Bair-Khosar Cave, Bc	metatarsal	OxA-17031						60,200		Stuart and Lister (2010)
Emine-Bair-Khosar Cave, Bc	metatarsal	OxA-17044						56,400 $\pm$ 2100		Stuart and Lister (2010)
Kryshataeva Cave	skull	MAMS-37004	16.9	3.2	10.3	42.2	15.4	17,900 $\pm$ 50	21,990–21,450	this study

Abbreviations: *cal BP* calibrated Before Present, *coll.* collagen

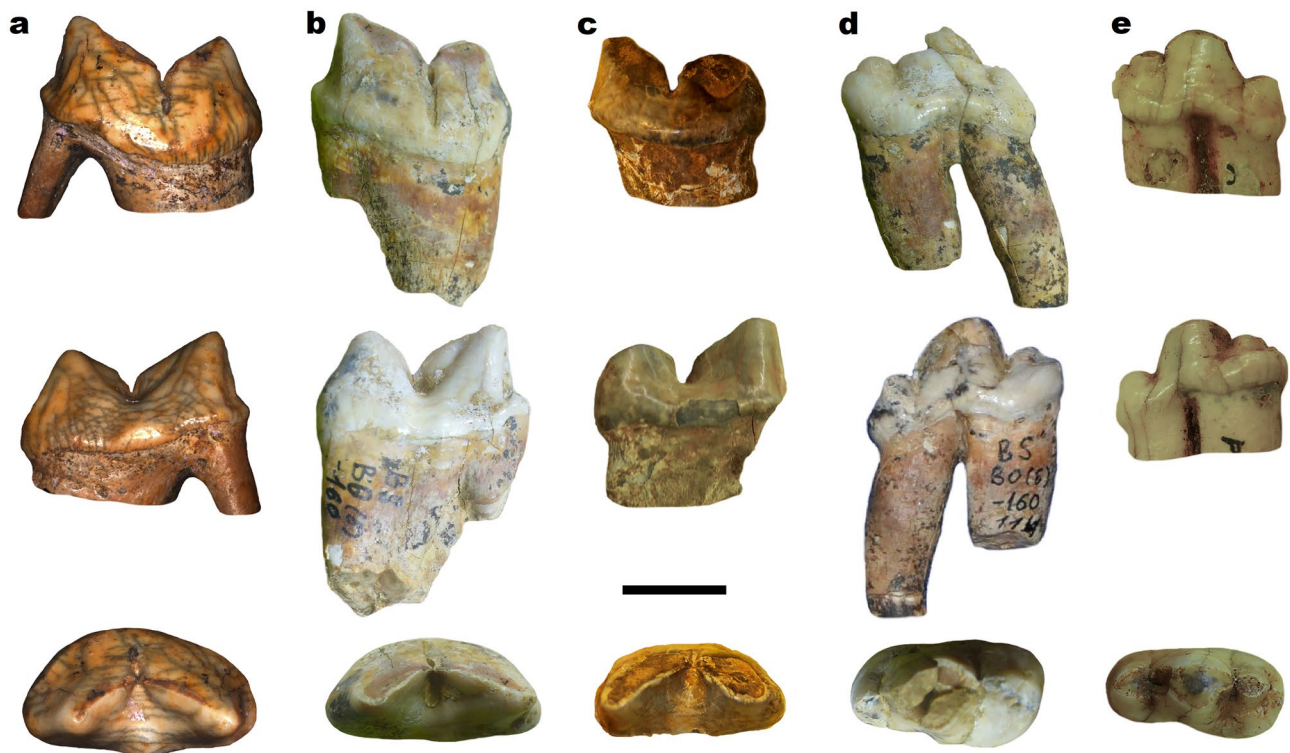
the calcaneus of *P. s. spelaea*. The facies articularis astragali lateralis is broad, shallow and separated from the facies articularis astragali medialis by a deep and wide groove. An oval and deep facies articularis cuboidea is connected distally with the facies articularis astragali medialis. The crescentic and flat sulcus for the tendon of the flexor hallucis longis is elongated and medially widened. The medial process is broad and elongated. It is triangular and situated almost vertically to the very massive corpus. Almost the entire surface of the medial process is covered by an oval and shallow facies articularis astragali medialis. The lateral process forms a thin and high crest running from the distal end to halfway along the corpus.

The calcaneus of the Sambir lion differs from that of *P. s. spelaea* in the following features. Its medial process is less elongated and more rectangular. The facies articularis astragali medialis on the medial process is less rectangular and flatter. The lateral process is developed more strongly, with a flat and longer facies articularis astragali medialis running more obliquely. The facies articularis cuboidea is deeper and does not contact the facies articularis astragali medialis. The only felid that could be mistaken with the calcaneus from Sambir is *Panthera gombaszoegensis* (Kretzoi, 1938). However, while similar morphologically, the calcaneus of this species is much smaller, with its length not exceeding 85 mm (Turner 1999).

The giant m1 from Sambir is oval and very robust (Fig. 2a), with its breadth to length ratio (B/L) being 56.8% (Fig. 2a). The value of this ratio corresponds to the values for *P. s. fossilis* and significantly exceeds those for *P. s. spelaea* (Table 3). The long and low paraconid holds a mesial margin shifted far mesially, whereas the distal wall of the slightly longer and much higher protoconid is noticeably sloped. The notch between the paraconid and the protoconid is deep, narrow, and V-shaped. The height measured on the lingual side from the bottom of the cingulum to that of the notch is 12.7 mm (Online Resource 1, Table S4). The crown is low and elongated in lateral view. A well-developed median bulge, situated on the lingual margin, rises into a small cusp-like structure. The strongly developed cingulum rises considerably upwards, buccally and lingually in the distal direction under the protoconid. The talonid is elongated and well developed (Fig. 2a).

### *Panthera spelaea spelaea* (Goldfuss, 1810)

The rest of the cave lion material was assigned to *P. s. spelaea*. Except for the individual from Bilykh Stin Cave (Fig. 2b and d), the Ukrainian specimens of this subspecies have moderate dimensions (Online Resource 1, Table S7). This is in good agreement with the general trend of decreasing size found in the European fossil record of the species (Argant et al. 2007; Marciszak et al. 2014, 2019, 2020a). It is best illustrated by



**Fig. 2** Isolated teeth of *Panthera spelaea* from Ukrainian sites in buccal (top row), lingual (middle row), and occlusal (bottom row) views: **a.** right m1 of *P. s. fossilis* from Sambir; **b.** right m1 from Bilykh Stin

Cave; **c.** right m1 of *P. s. spelaea* from Volia-Homuletska; **d.** right p4 from Bilykh Stin Cave (FCNU-G BS-114); **e.** right p4 of *P. s. spelaea* from Volia-Homuletska. Scale bar equals 20 mm

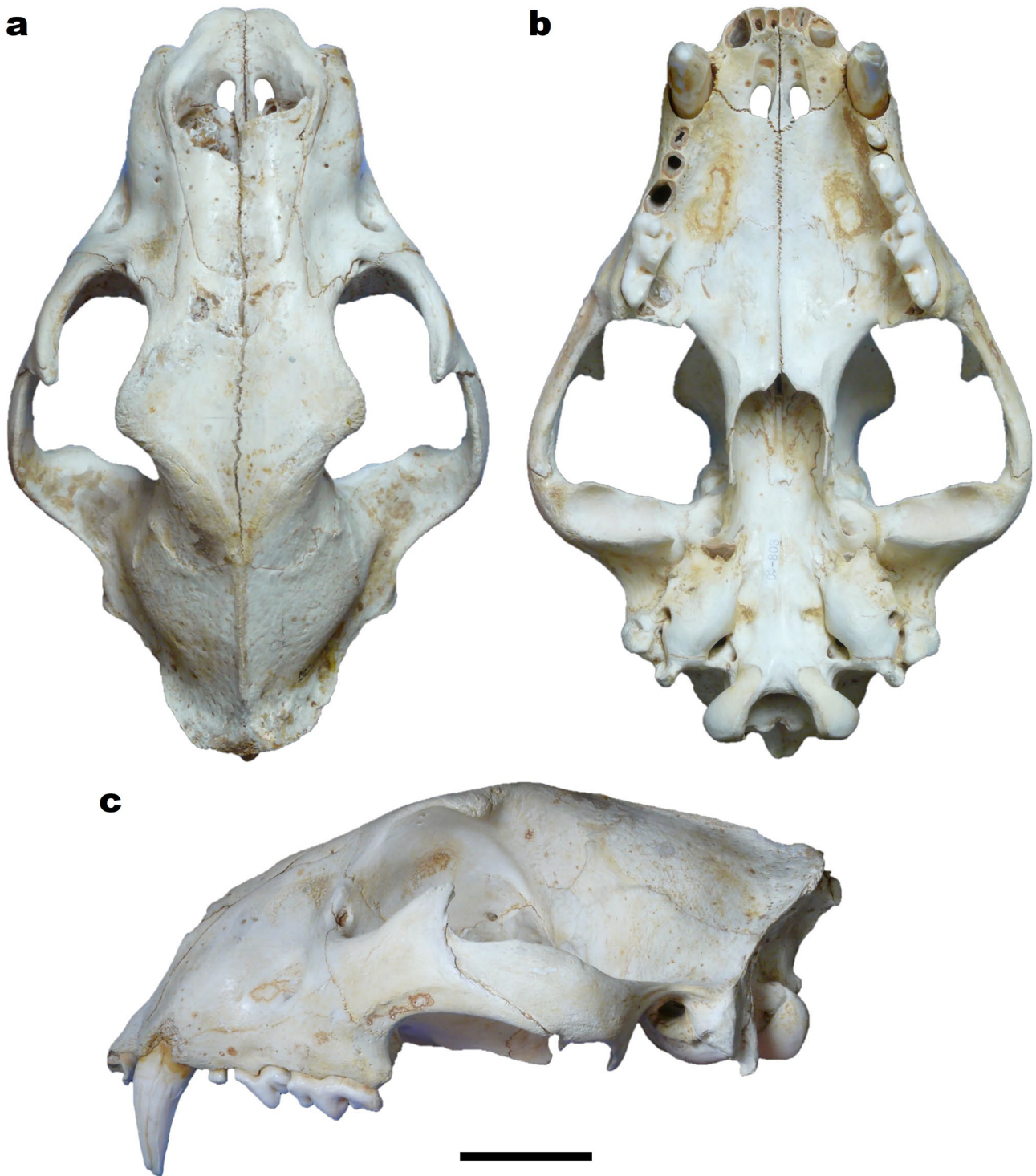
NMNHU-P OF-803/1964 and OF-806/1964, a skull of a very small lioness from Kryshtaleva Cave, which belongs to a fully grown 3–5-year-old female (Fig. 3). Its individual age was estimated from closed sutures and unworn teeth. The sex was determined from the small size, gracile build, low and short sagittal crest, narrow zygomatic arches, and narrow canines (Fig. 3).

The most peculiar feature of the small lioness specimen from Kryshtaleva Cave is its extremely small dimensions, which are far below the size range of Eurasian cave lions and in the lowermost range of modern lionesses (Online Resource 1, Table S7). The total length of the skull (~268 mm) is even smaller than in *P. gombaszoegensis*, whose skull length varied within 273–330 mm in the Early Pleistocene *P. g. toscana* (N=3; Kotsakis and Palombo 1979; Koufos 1992) and within 280–300 mm in *P. g. gombaszoegensis* (N=3; Tournepiche 1996; Argant and Argant 2011). The Kryshtaleva lioness is even smaller than some individuals of the leopard *Panthera pardus* (Linnaeus, 1758) whose skulls can reach about 280 mm (Prater 1921; Kiabi et al. 2002; Moqanaki et al. 2010), even if the Pleistocene European skulls of the species very rarely exceed 250 mm (Kotsakis and Palombo 1979 and references therein). There is another European find of a very small lion, the skull from the loess deposits of a quarry near Ghidfalău, Romania (Samson and Kovács 1967), which is also dated to the latest Late Pleistocene. Both skulls have almost the same morphology.

The skull NMNHU-P OF-803/1964 has a moderately long rostrum slightly widened at canines and P2s. The incisor row is broad and curved; zygomatic arches are narrowly spaced. The temporal region is proportionally short and wide and the postorbital constriction is broad. In lateral view, the frontal profile is convex, forming a regular arch and gently marked concavity in the middle of the frontal part. The orbits are large and rounded, while the mastoid processes are broad and widely spaced (Fig. 3). The tympanic bullae are quite small but well inflated, and strongly convex with a moderately large tympanic chamber. The canines are elongated but narrow, typical for female lions. Between C1 and P2, there is a small diastema, while the other teeth (P3, P4, and M1) are tightly spaced.

The present P2 is a small, narrow, one-rooted tooth with an oval crown, straight buccal margin, and moderately developed median convexity on the lingual side. The narrow and elongated P3 has well-developed mesial and distal cingulum ridges. The transition between the narrower mesial and wider distal parts of the crown is weakly marked. The lingual margin is almost straight, while the buccal margin is gently concave, with weak median convexity. The paracone is proportionally long, low and oval. It is located exactly medially followed by a moderately large, rounded and low metastyle. The protocone is present as a rudimentary and





**Fig. 3** Cranium of *Panthera spelaea spelaea* NMNHU-P OF-803/1964 from Kryshtaleva Cave. **a.** dorsal view; **b.** ventral view; **c.** lateral view. Scale bar equals 50 mm

poorly visible structure, located mesio-lingually. The distinction between the paracone and metastyle, as well as between the metastyle and weak distal cingulum, is well pronounced (Fig. 3).

The elongated and narrow P4 possesses a rounded, relatively reduced and low protocone shifted more disto-lingually. There is no sign of the preparastyle; there is only a parastyle-like small structure formed by a weakly



**Fig. 4** Mandibles of Late Pleistocene *Panthera spelaea spelaea* from Ukraine. **a.** Kryshtaleva Cave (NMNHU-P OF-806/1964) in occlusal (top) and buccal (bottom) views; **b.** Molodova 1 (KIUS MOL 101) in buccal (top), lingual (middle), and occlusal (bottom) views; **c.** Kodak (NMNHU-P OF-645/3197) in buccal (top), lingual (middle),

and occlusal (bottom) views; **d.** Kodak (NMNHU-P OF-646/3541) in buccal (top), lingual (middle), and occlusal (bottom) views; **e.** Emine-Bair-Khosar (NMNHU-P Bj-104) in buccal (top) and lingual (bottom) views. Scale bar equals 50 mm

developed cingulum. The lingual margin is almost straight, while the crown is slightly convex buccally. The parastyle is moderately large, high and oval. It is also well separated from the paracone by a deep and sharply pointed valley. The constriction between the parastyle and the paracone is notable in occlusal view. The paracone is proportionally short and low, and the metastyle is slightly longer and lower than the paracone. The bulging of the distal part of the crown is weakly marked. The M1 is missing; its alveolus indicates a small, oval, two-rooted tooth oriented perpendicularly to P4 (Fig. 3).

The mandible in the Kryshdaleva lioness (NMNHU-P OF-806/1964) is elongated and slim, with two parallel edges thickening distally (the height is 39.5 mm anterior to p3 and 42 mm posterior to m1) (Fig. 4a). The symphyseal part is long and narrow; the lower margin of the mandible is straight. There are three mental foramina, two of which are located under the moderately long diastema and the third is under the mesial root of p3. The anterior section of the masseteric fossa is deep, well-outlined and narrow, extending forward under m1. The triangular and proportionally short ramus has moderately developed muscle attachments and a strongly developed angular process (Fig. 4a).

The two-rooted p3 is narrow and oval, with a moderately developed, low and rounded protoconid located in the centre. The paraconid is absent, while the hypoconid is strongly reduced and present as a rudimentary, weakly visible structure. The medially positioned hypoconid rises slightly distolingually. It is closely associated with the protoconid and moderately separated from the surrounding cingulum, which is better developed only on the distal wall. In occlusal view,

the buccal margin is slightly convex, and the lingual margin of the distal half is gently expanded. The transition between the narrower mesial and wider distal parts is poorly marked.

The narrow and long p4 has a slightly convex buccal margin, while the lingual margin is slightly expanded and forms a small smooth area. The medially positioned protoconid is long and low. The cuspids are moderately large (with the hypoconid being larger), rounded, and low. The hypoconid is poorly separated from the strong distal cingulum, whereas the paraconid is well separated from the protoconid by a broad V-shaped valley (Fig. 4a).

The oval and high-crowned m1 is narrow, with the B/L ratio being 49.2%. The paraconid is long and low, with its mesial margin poorly shifted mesially (Fig. 4a). The protoconid is slightly longer and higher than the paraconid and its distal wall is almost vertical. The notch between the paraconid and protoconid is deep, wide and V-shaped. The height of the notch, measured on the lingual side from the bottom of the cingulum, is proportionally low. A weak median bulge is situated on the lingual margin between the paraconid and protoconid on the left m1, while it is absent on the right m1. The lingual margin is almost straight, while the buccal one is moderately convex. The weakly developed lower margin of the cingulum rises gently upwards buccally in the distal direction under the protoconid. It does not rise on the lingual side and creates almost a straight line. The talonid is strongly reduced (Fig. 4a).

Morphologically, the skull from Kryshdaleva Cave corresponds to the evolutionary advanced cave lion from the latest Late Pleistocene (MIS 3–2). In contrast to extant *P. l. persica*, the Kryshdaleva lioness possesses a distinctly

**Table 3** Selected dental ratios for five temporal samples of *Panthera spelaea* in comparison with cave lions from several Ukrainian sites

	L pr/L p4		Bd/L p4		B/L m1		L p4/ L m1	
	M (Min–Max)	N	M (Min–Max)	N	M (Min–Max)	N	M (Min–Max)	N
MIS 20–12	<b>45.8</b> (42.7–48.5)	16	<b>54.7</b> (47.3–58.6)	21	<b>56.6</b> (50.2–59.1)	48	<b>97.6</b> (87.3–101.3)	15
MIS 11–9	<b>48.1</b> (44.9–52.8)	13	<b>52.2</b> (48.5–57.1)	16	<b>54.0</b> (50.2–56.8)	25	<b>97.1</b> (90.7–103.6)	13
MIS 8–6	<b>48.6</b> (43.2–50.2)	17	<b>50.4</b> (45.2–56.9)	21	<b>51.9</b> (47.7–57.1)	40	<b>95.7</b> (88.3–105.3)	11
MIS 8–6	<b>51.4</b> (44.8–54.1)	14	<b>49.4</b> (41.8–57.3)	26	<b>51.0</b> (46.4–56.9)	40	<b>93.3</b> (85.7–111.2)	18
MIS 4–2	<b>52.2</b> (44.5–56.3)	123	<b>49.8</b> (42.4–60.7)	177	<b>46.1</b> (41.8–53.7)	221	<b>92.4</b> (83.3–107.6)	118
Sambir					<b>56.8</b>	1		
Bilykh Stin Cave	<b>47.3</b>	1	<b>53.6</b>	1	<b>50.0</b>	1	<b>93.8</b>	1
Kremenchuk	<b>52.9</b>	1	<b>47.1</b>	1	<b>47.1</b>	1	<b>90.8</b>	1
Volia-Homuletska	<b>52.3</b>	1	<b>48.8</b>	1	<b>47.5</b>	1	<b>93.9</b>	1
Kodak	<b>49.9</b> (48.1–51.7)	2	<b>53.1</b> (52.6–53.6)	2	<b>52.3</b> (52.2–52.3)	2	<b>88.0</b> (86.7–89.3)	2
Rudky			<b>51.6</b>	1	<b>53.3</b>	1	<b>94.3</b>	1
Molodova 5	<b>47.8</b> (47.4–48.1)	2	<b>52.4</b> (52.2–52.6)	2	<b>47.7</b> (47.0–48.4)	2	<b>101.1</b> (100.0–102.1)	2
Kryshdaleva Cave	<b>49.0</b> (48.6–49.4)	2	<b>47.9</b> (46.7–49.0)	2	<b>49.2</b>	2	<b>98.5</b> (97.3–99.6)	2
Emine-Bair-Khosar	<b>54.9</b>	1	<b>48.9</b>	1	<b>50.4</b>	1	<b>94.7</b>	1

Abbreviations: *B* breadth, *Bd* distal breadth, *L* length, *M* mean, *Max* maximum value, *Min* minimum value, *MIS* Marine Isotope Stages, *N* number of individuals





**Fig. 5** Postcranial bones of *Panthera spelaea spelaea* from Ukraine. **a.** left humerus NMNHU-P 10–789 from Kaniv (from left to right: cranial, caudal, lateral, medial views); **b.** left radius FCNU-G BS 123 from Bilykh Stin Cave in caudal (left) and cranial (right) views; **c.** left scapula NMNHU-P 56–6660 from Mezhyrich in lateral (left) and medial (right) views; **d.** right talus FCNU-G BS 54 from Bilykh Stin Cave in dorsal (left) and ventral (right) views; **e.** left metacarpal

3 FCNU-G BS 113 from Bilykh Stin Cave (from left to right: dorsal, ventral, medial, lateral views); **f.** left metatarsal 4 FCNU-G BS 119 from Bilykh Stin Cave (from left to right: dorsal, ventral, lateral, medial, ventral views); **g.** left metacarpal 2 FCNU-G BS 120 from Bilykh Stin Cave (from left to right: dorsal, medial, lateral views). Scale bar equals 70 mm

less inflated neurocranium and tympanic bullae, noticeably broader postorbital constriction, undivided infraorbital foramen (typical for the cave and modern south African lions, but uncommon in Asian and North African lions; Yamaguchi et al. 2009), P3 with weakly developed metastyle, and P4 without preparastyle and with reduced protocone (Figs. 3 and 4). Therefore, we assign this specimen to *P. s. spelaea*.

The Kryshtaleva skull is morphologically similar to a well-preserved skull of the cave lion from Chernihiv, measured and illustrated by Pidoplichko (1956). The Chernihiv skull (A-34) is larger (375 mm) but falls into the range of the Late Pleistocene lions, especially those dated to MIS 4–2. Despite the relatively small dimensions, the skull possesses quite massive canines, which indicate a male. For the last glacial, the total skull length of *P. s. spelaea* males does not exceed 400 mm (Marciszak et al. 2014). A good example of a typical, moderately sized specimen from the European last

glacial dated to about 47 kyr BP is a male skull from Siegsdorf (L = 384 mm) (Gross 1992; Stuart and Lister 2011). The Chernihiv specimen cannot be assigned to the Middle Pleistocene lions because it is smaller and has a proportionally shorter and broader snout, larger orbits, shorter and wider temporal and mastoid areas, broader incisor row and narrower teeth.

Two isolated teeth from Bilykh Stin Cave, p4 (FCNU-G BS-114) and m1 (FCNU-G BS-129), show a number of more primitive features indicating an older age than that of the lioness from Kryshtaleva Cave. These specimens are much larger, more robust, and match in size the late Middle and Late Pleistocene lions. The large and broad p4 has a short, high and medially positioned paraconid. The protoconid length to total length ratio is 47.4%, which agrees with the values for the Middle Pleistocene lions rather than Late Pleistocene ones (Table 3). The protoconid is larger than the hypoconid, rounded and separated from



the paraconid by a shallow and wide, V-shaped valley. It is situated exactly in the middle of the tooth (Fig. 2d). The smaller hypoconid is closely associated with the protoconid and oriented more disto-buccally. It is also more oval and lower than the protoconid. The distal cingulum is strongly developed, which makes a strongly marked ridge; there is a pronounced border between the hypoconid and cingulum ridge. The distal part of the crown is strongly elongated on the lingual side towards the distal root and creates a long, almost flat, triangular surface. The transition from the narrower mesial half to the wider distal part is well marked. The distal half of the crown noticeably bulges buccally and lingually. While both margins of the mesial half are straight, the margins of the distal half are moderately convex. The mesial and distal margins are blunt, with well-developed cingula, which create a thin, but well-defined wall (Fig. 2d).

The m1 is oval and moderately wide since the breadth to length index is 50%. The paraconid is long and low, with the mesial margin shifted far mesially (Fig. 2b). The protoconid is slightly longer and distinctly higher than the paraconid and its distal wall is sloped. The notch between the main cusps is deep, wide, and V-shaped. The height measured on the lingual side from the bottom of the cingulum to that of the notch between the paraconid and the protoconid is large. The crown is low and relatively elongated in lateral view. The median lingual bulge is moderately developed. The buccal side is moderately convex. The mesial and distal margins are sharp. The strongly developed lower margin of the cingulum rises considerably upwards, buccally and lingually in the distal direction under the protoconid (Fig. 2b). The talonid is elongated and well-developed. The tooth is longer than p4 (Table 3).

All of the above dental features indicate an evolutionarily somewhat less-advanced lion and an age older than the Late Pleistocene. The main cusps of the Bilykh Stin teeth are still quite high, their crowns are rather broad, and some of their parts are weakly reduced, such as the additional cuspids in p4 and the talonid in m1 (Fig. 2b and d). At the same time, these teeth demonstrate some progressive features, e.g., a rather narrow m1, which is longer than p4 and has a weak median lingual bulge. The Bilykh Stin lion cannot be classified as *P. s. fossilis*. Morphologically, this lion resembles *P. s. intermedia* whose m1 was described as being smaller, narrower and with a less-developed median bulge, compared to *P. s. fossilis* (Argant and Brugal 2017). All these traits are observed in the m1 from Bilykh Stin Cave. Three complete metapodials from Bilykh Stin Cave (mc2, mc3, and mt4; Fig. 5) are large and robust, but they are more gracile and have less-developed muscle attachments than in *P. s. fossilis*; these features also suggest *P. s. intermedia* (Argant and Brugal 2017), although the limited material does not allow a more definite assignment.

The exact stratigraphic position of the lion from Bilykh Stin is unknown. All direct dating methods, such as radiocarbon or uranium–thorium, failed to provide any results. The ursid material found together with lions belongs to a deningeroid bear, with numerous primitive features different from spelaeoid ones. All this might indicate that the Bilykh Stin lion is of late Middle Pleistocene age, somewhere between MIS 8 and MIS 6, thus indirectly supporting its attribution to *P. s. cf. intermedia*.

The isolated humerus NMNHU-P 10–789 from Kaniv, with dimensions comparable with the largest lions, cannot be assigned to a particular subspecies (Fig. 5a). Its stratigraphic position is unclear, and it could be late Middle or Late Pleistocene (Ridush et al. 2020a, b). Therefore, we identify this specimen as *P. spelaea* ssp.

### Body mass estimates

Body mass estimates from linear dimensions are inevitably very approximate (Hemmer 2003). The case from Kenia, where Meinertzhagen (1938) measured three lions at the withers of 86 cm each, showed an extent to which body mass can vary (122, 158, and 181 kg) in the same linear size class. Furthermore, extant male lions are 15% longer but more than 50% heavier than females (Schaller 1972). The sexual dimorphism in body mass of the cave lions is even more conspicuous, with males being 31% longer and 80% heavier than females (Turner 1984; Baryshnikov and Boeskorov 2001; Hemmer 2011; Sabol et al. 2018).

Nevertheless, we attempted to estimate body mass of Ukrainian lions using mostly craniodental and occasionally postcranial material. The body mass estimates for the directly examined material (from Sambir, Bilykh Stin Cave, Kodak and Kryshtaleva Cave) and several previously published specimens are presented in Table 4.

An estimate for the Sambir lion (based on calcaneus length) looks less reliable than that inferred from m1 size. However, the latter is probably underestimated and the Sambir lion might have had a body mass exceeding 500 kg. It is unlikely that this value represents the extreme upper mass range, as in the case of record-sized individuals of living felids. Such exceptional specimens are too rare to appear in the fossil record (Christiansen and Harris 2009; Wheeler and Jefferson 2009).

The Bilykh Stin lion turns out to be very large, although smaller than the specimen from Sambir. In general, a body mass between 300–330 kg seems to be the most credible for this lion. The Late Pleistocene specimens are smaller and their estimated body mass range (~150–260 kg) suggests strong sexual dimorphism. Taking into account the underestimation of body mass when using m1 as a predictor, a range of 140–180 kg for females and 200–300 kg for males seems reliable.

Finally, the body mass of the Kryshtaleva lioness was estimated as ranging from 83 kg (based on CBL) to nearly

**Table 4** Body mass of lions from several Ukrainian sites (in kg) estimated from skeletal and dental indicators

Site	Cranial or post-cranial	m1 L	m1 L×B
Sambir	912.0	353.2	440.0
Bilykh Stin Cave	491.5–515.9	286.5	292.6
Chernihiv	221.6		
Kryshtaleva Cave	83.1–128.9	143.0–149.9	141.3–148.3
Molodova 5	176.1	198.0	183.0–191.5
Kodak		226.6	247.6
Rudky		148.2	165.4
Kremenchuk		260.4	242.5
Mayaky	176.1–191.7		
Olviya (Pontic Olbia)		88.0	82.4

Abbreviations: *L* length, *B* breadth

150 kg (on L m1). The Kryshtaleva lioness has an extremely small skull while its lower carnassials are 25.8 and 26.2 long. This specimen seems to illustrate that ‘...small individuals have relatively bigger teeth than larger specimens’ (Lundholm 1952:24). This may lead to some overestimation of body mass based on m1 length in this case (see Table 4). In sum, a mass of 100–120 kg seems an appropriate approximation for the Kryshtaleva lioness, taking into account a more massive build than in extant lions.

## Discussion

### Decreasing size in *Panthera spelaea*: From giants to dwarfs

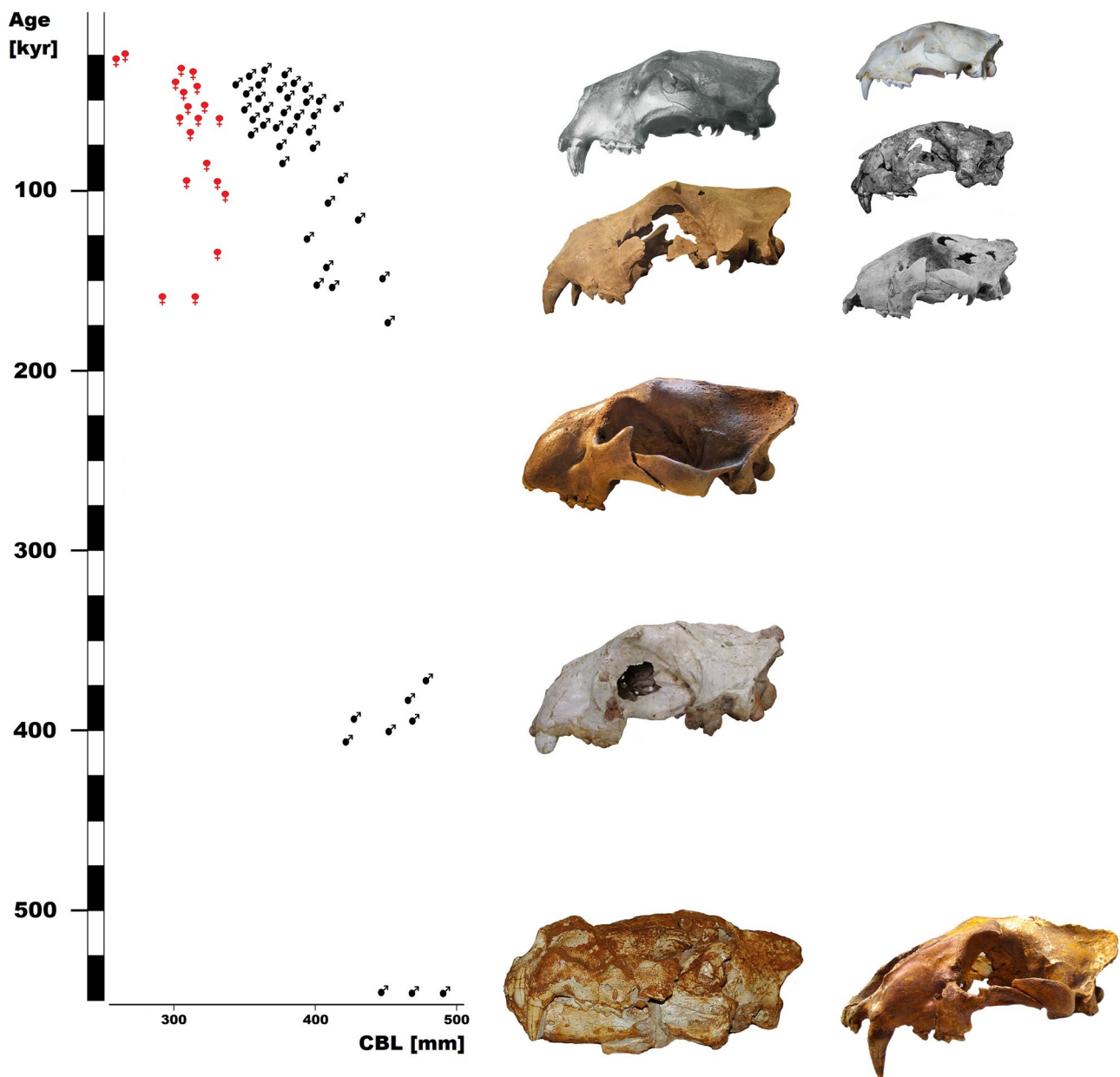
The material of *P. spelaea* from Ukraine agrees with a trend of decreasing body size found in the cave lion lineage by several authors including Kurtén (1960, 1968), Schütt (1969), Schütt and Hemmer (1978), Argant (1988, 1991, 2000), Argant et al. (2007) and Marciszak et al. (2019, 2020a, b). As Argant et al. (2007: 127) put it, “Size drops steadily in the course of time (with some exceptions, however) until it reaches that of the living lion”. A size change pattern through time can be detected and investigated by comparing dimensions (e.g., skull length) from a number of sites (Fig. 6). During the Middle Pleistocene, the size of *P. spelaea* varied only slightly. Substantial size changes began in the Late Pleistocene (Marciszak et al. 2014, 2019, 2020a).

Between 48 and 45 kyr ago, *P. spelaea* populations experienced a dramatic decline in genetic diversity, which resulted in a genetic bottleneck (Barnett et al. 2009). Interestingly, the decline in body size became stronger during MIS 3. Among moderate-sized cave lions, like those from Siegsdorf or

Chernihiv (Dietrich 1968; Gross 1992; Marciszak et al. 2014, 2019), appreciably smaller individuals started to appear. Their dimensions suggest a more gracile stature (Altuna 1972; Clot et al. 1984; Pautret-Homerville et al. 2011) and are comparable with medium-sized individuals of extant African lions (Fig. 6).

The total skull length in the mid-Middle Pleistocene (MIS 20–12) *P. s. fossilis* males from Château (484.7 mm and 465.0 mm) and Mauer (452.0 mm) exceeds the total skull length in later lions. The late Middle Pleistocene (MIS 11–9) male skulls from Crayford (450.0 mm), Petralona Cave (426.0 mm), Azé Cave (417.4 mm), Mokhnevskaya Cave (~475.0 mm), Moggaster Cave (~445.0 mm) and L’Herm Cave (410.0 mm) are more diverse and smaller. The skulls dated to MIS 8–6, from Edingen (~440.0 mm), San River (451.0 mm), Lezetxiki (421.5 mm), Niedźwiedzia Cave (416.4 mm) and Romain-la-Roche (400.9 mm) are still large, but appreciably smaller than Middle Pleistocene ones. Typical male skulls from the last glacial do not exceed 400.0 mm in total length. The only exception is the largest skull (holotype) from Zoolithen Cave having a total length of 417.0 mm (Kempe and Döppes 2009). This trend of decreasing size is better documented in male skulls because finds of females are much scarcer. The Eemian lioness skull from Zandobio is 324 mm long, while the Late Pleistocene female skull from Srbsko Chlum-Komín is 303 mm long. And the smallest is the 22-kyr-old skull of the Kryshtaleva lioness described in this study, which is only 268 mm long (Fig. 6).

The same trend of decreasing size was found when analysing the m1 length (Fig. 7). While the size of the premolars does not correlate with body mass and size, the dimensions of the m1 allow estimating the size of the lion with a 95% probability (Van Valkenburgh 1990; Van Valkenburgh and Sacco 2002). The lower carnassial also allows identifying the sex of particular individuals because large pantherine cats have considerable sexual dimorphism, and adult males are usually much larger than adult females. It should be noted, however, that the large lions can be more reliably sexed than the small- or average-sized ones. On the one hand, there is some size overlap between sexes in extant *P. leo*. Gross (1992) found that the mean of the m1 length in male lions is 28.3 mm (25.5–32.5 mm; N = 17), while the mean for females is 25.8 mm (24.5–28.0 mm; N = 17). On the other hand, Wheeler and Jefferson (2009) found almost no overlap in sexes of *P. atrox* from Rancho La Brea and Natural Trap Cave, which is comparable in size with the larger individuals and subspecies of *P. spelaea*. According to Wheeler and Jefferson (2009: 440–441, table 2), the mean length of the m1 is 31.2 mm (29.5–34.0 mm; N = 31) in males and 27.5 mm (25.1–29.1 mm; N = 20) in females. Meachen-Samuels and Binder (2010) found a small overlap in the mandible size between sexes of *P. atrox*. It may be cautiously assumed that the m1 size overlaps in sexes of *P. spelaea* – even if this overlap is smaller than in extant *P.*



**Fig. 6** Decreasing size in the evolution of *Panthera spelaea* illustrated by skull length. Left column (males), from bottom to top: Château (from Argant and Argant, 2018: fig. 7); Petralona (from Baryshnikov and Tsoukala, 2010: fig. 21); San, Niedźwiedzia Cave,

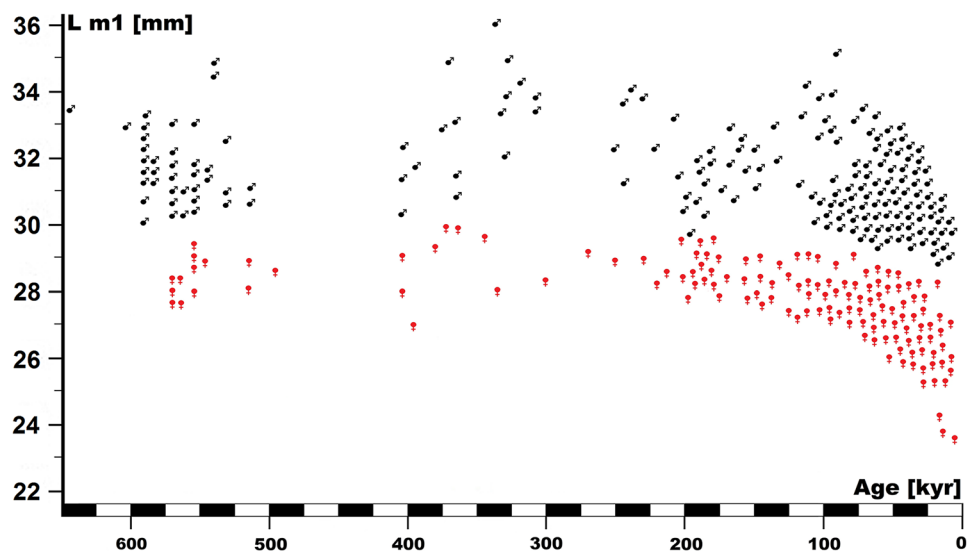
Siegsdorf (from Gross, 1992: fig. 1/11). Right column, bottom: Mauer. Right column (females), bottom to top: Zandobbio (from Bona, 2006 fig. 1B); Srbsko Chlum-Komín (from Diedrich 2007: fig. 5A); Kryshaleva Cave (this study)

*leo* – but the m1 longer than 29 mm (and up to 36 mm) most probably belongs to a male.

We found a decrease in size (as inferred from the lower carnassial length) in both sexes of the cave lion. During the Middle Pleistocene, differences in m1 length were rather insignificant among *P. spelaea*, with lions from about 700–300 kyr BP being only slightly larger than those from 300–100 kyr BP. It should be noted, however, that *P. s. fossilis* has smaller teeth proportionally to the body size, albeit more robust. The total

length of the m1 did not change rapidly until 50 kyr BP when, according to Barnett et al. (2009), the lion populations underwent a dramatic decline in genetic diversity. During the period 45–15 kyr BP, much smaller individuals appeared, comparable with medium-sized extant lions. These are, e.g., the m1 specimens from Bois de Cantet (Clot 1980), Azoleta Cave (Castaños 2005), and Ghidfalucariera (Samson and Kovacs 1967) (Fig. 7).

**Fig. 7** Decreasing size in the evolution of *Panthera spelaea* illustrated by m1 length. For references used, see Material and methods



Among the material from Ukraine, the isolated m1 from Sambir ( $L = 34.7$  mm) represents a male of Middle Pleistocene *P. s. fossilis*, a cave lion subspecies regarded as one of the largest felids that ever lived (Kurtén 1968; Argant et al. 2007). The m1 from Bilykh Stin Cave, representing a male of presumably late Middle Pleistocene *P. s. intermedia*, is smaller (32.4 mm). A larger sample of lower carnassials of Late Pleistocene *P. s. spelaea* demonstrate somewhat smaller dimensions than in the earlier forms, but their sexual determination in some cases cannot be as reliable as for the lions from Sambir and Bilykh Stin Cave.

The specimen from Molodova 5 ( $L\ m1 = 28.7$  mm), from the latest part of the late Middle Pleistocene (end of MIS 6, sensu Ridush and Popiuk 2020a) is probably a lioness. The specimens from Kodak (30.0 and 30.1 mm) and Kremenchuk (31.4 mm) were cautiously sexed as males, while those from Rudky (26.1 mm) and Molodova 1 (25.6 mm) as females. These teeth are still moderately large, with the size typical for the Late Pleistocene. Finally, from the second part of the Late Pleistocene (MIS 3 and younger), we have some very small specimens, e.g., that from Emine-Bair-Khosar (24.6 mm). In sum, both the cranial and dental material of *P. spelaea* from Ukraine follows a trend of decreasing body size (Figs. 6 and 7).

The cave lion was considered by many authors (e.g., Argant 1988, 1991 or Hemmer 1974, 2001, 2003, 2004, 2011) to be extremely massive. Hemmer (2011: 205) stated that the weight of *P. spelaea* was 160–180% of the body mass of the South African *P. leo* of similar linear size. Argant (1988), based on the size of the scapula (264 mm long), humerus (389.4 mm long), and radius (354 mm long), estimated the linear size of the Azé lion as 350 cm long and 130 cm high, and the weight of more than 300 kg. The specimen from Bilykh Stin was probably as big or slightly bigger. In this aspect, the size of the Sambir lion, with a 34.7 mm

long m1, is noticeably larger, and for this individual a head and body length of 250–270 cm and a shoulder height of 140 cm can be proposed. It is also the size proposed for large specimens of *P. s. fossilis* and *P. atrox* by previous authors (Hemmer 2011). Late Pleistocene specimens such as those from Chernihiv, Kodak, or Kremenchuk, although still large, are much smaller than the Sambir lion and metrically comparable with the Siegsdorf lion, which was estimated to be 200–210 cm long and 120 cm high (Gross 1992). The Kryshtaleva lioness was estimated to have a head and body length of about 120–130 cm and a shoulder height of 70–75 cm.

Cave paintings, which could be used for inference of the external appearance of lions, have not been reported from Ukraine. The French and Spanish Paleolithic art caves (Crémades and Laville 1995; Chauvet et al. 1995; Spassov and Stoychev 2005; Cueto et al. 2016) show maneless lions of great size and bulky stature or having only slightly longer hairs on the neck, shoulders and chest. The stature of earlier *P. spelaea* was even bulkier, so for most of their history cave lions were distinctly larger and more massive than their representatives from the latest part of the last glacial and than their congeneric *P. leo* (Fig. 8).

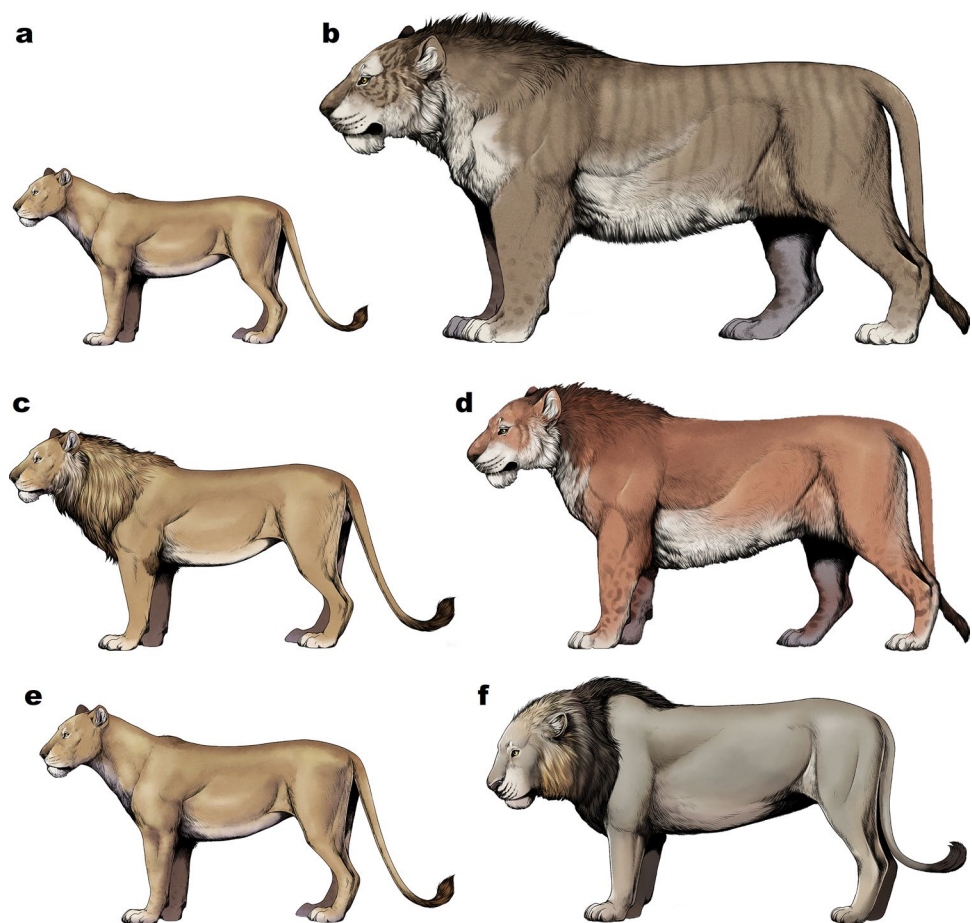
### Extinction of *Panthera spelaea*: The king is dead

The cave lion went extinct about 18–17 kyr ago (Stuart and Lister 2010). In Ukraine, the available radiocarbon dates suggest the species survival to at least 22–21 cal kyr BP (Kryshtaleva skull directly AMS-dated in this study) and probably to 18–17 cal kyr BP (indirect dates for Mezhyrich; Haesaerts et al. 2015).

Overall, the cave lions were dependent on the availability of large and mostly moderately fast-moving prey (Bocherens et al. 2011; Diedrich 2014, 2017; Bocherens 2015). The evolving climate and vegetation during the Late Pleistocene



**Fig. 8** Size comparison of Ukrainian lions and the extant southern lion. **a.** *Panthera spelaea spelaea* (♀) from Kryshtaleva Cave; **b.** *Panthera spelaea fossilis* (♂) from Sambir; **c.** *Panthera leo persica* (♂) from Mayaki; **d.** *Panthera spelaea spelaea* (♂) from Chernihiv; **e.** *Panthera leo melanochaita* (Smith, 1842) (♀) from Kruger National Park; **f.** *Panthera leo melanochaita* (♂) from Kruger National Park. Shown to the same scale. Drawings by W. Gornig



promoted habitat fragmentation (Huntley 1988, 1990, 1992; Starkel 1991; Grove and Rackham 2001; Magri et al. 2007; Masseti and Mazza 2013); and the patches of Pleistocene vegetation acted as refugia for the Pleistocene fauna (Stewart and Lister 2001; Reumer 2007). Populations enclosed in these fragmented habitats reacted to environmental changes by evolving towards smaller-bodied members. In other words, the narrower species ranges produced smaller ungulates. Indeed, a trend of decreasing body size can be observed in several large mammals during the Late Pleistocene (Reumer 2007).

Both decreasing body size and eventual extinction of the cave lion might be explained by their ecological response to harsh environmental conditions and decline in prey abundance. This is exemplified by the case of West Africa, where the short-maned, gracile, and small Senegal lion existed in harsh habitats with a limited number of large ungulates (Lupták 2009). A similar scenario has been proposed for the small Beringian and Eastern Siberian cave lions, previously considered as separate subspecies *Panthera spelaea vereshchagini* Baryshnikov et Boeskorov, 2001 (Baryshnikov and Boeskorov 2001). Beringian lions were only slightly larger than the dwarf lionesses from Kryshtaleva Cave or Ghidfaläu.

Baryshnikov and Boeskorov (2001) suggested that less favourable climatic and habitat conditions forced the cave lion to evolve into a smaller form requiring less energy to sustain (Carbone et al. 1999). This evolutionary adaptation could have allowed the species to maximise its foraging effort and survive in those areas. The main climatic conditions that triggered these responses were low winter temperatures, a long duration of snow cover and an elusive or growth-limiting food base (Baryshnikov and Boeskorov 2001). Diminution in size is also known in some other Late Pleistocene and extant large carnivores, e.g., in the brown bear (Baryshnikov and Boeskorov 1998; Marciszak et al. 2015) and island tiger (Mazák 1979, 1981).

The above explanation can also be the case of the Ukrainian cave lions, at least for the Kryshtaleva lioness. As the Last Glacial Maximum was approximately 22 kyr BP, the Crimean population of *P. s. spelaea* must have been the one forced south by the spreading ice sheet. It can be speculated that similarly to the case of Beringian lions, less suitable climatic conditions and a smaller prey base favoured the presence of such small lions.

Whether human hunting pressure had any impact on the extinction of cave lions is open to debate. So far there is no

direct evidence to support or refute the idea that humans had such a negative impact on the fauna that it resulted in a ‘pre-historic overkill’ sensu Martin (1984). Reduced prey density and the expansion of dense forests, coupled with the increase in moisture after the last glacial maximum (Zanon et al. 2018; Spötl et al. 2021), might have contributed to the *P. spelaea* range contraction and population decline, with human hunting accelerating its extinction (Stuart and Lister 2010).

The carnivoran body size is a great advantage in conflicts between carnivorans, and large adult males almost always dominate their competitors (Eaton 1979; Diedrich 2021). In this respect, the smaller body size of the last lions might result in their being more vulnerable to attacks by other predators and less effective in conflicts with them. Analyses of isotope values suggest that the wolf might have outcompeted the cave lion in accessing prey species in the post-LGM period (Bocherens et al. 2011; Bocherens 2015). The wolf, as a smaller but agile, highly mobile, and ecologically versatile species, could roam broader areas and cover much larger distances searching for food. Herds of large ungulates, such as reindeer, horses, and bovids, may have been frightened and chased away by packs of hunting wolves. It might have caused potential prey to be virtually absent or available in very limited numbers. In addition, the cave lion was a territorial felid and this might have been a disadvantage in interspecific competition. When co-existing with the wolf, the cave lion could have been limited to the prey (e.g., reindeer and cave bears) not taken by these gregarious predators (Bocherens et al. 2011; Bocherens 2015; Marciszak et al. 2020a, b).

### Holocene *Panthera leo* of Ukraine: Long live the king

The Ukrainian fossil and zooarchaeological record suggests a 10–12-kyr gap between the disappearance of *P. s. spelaea* and the appearance of *P. leo* in the region. After its entering Eurasia, the extant lion formed a contiguous range until human expansion along the Nile and the Sinai Peninsula started to separate it into isolated populations ca. 6.0–5.5 kyr BP (Yamaguchi et al. 2004; Schnitzler 2011; Kitchener et al. 2017; Daróczy-Szabó et al. 2020). A fragmentary upper canine from the Bulgarian settlement site Karanovo has been reported as the earliest European find of *P. leo*, archaeologically dated to 8.0 kyr BP. However, given the absence of any other similarly dated European finds, this record is now treated with caution (Bartosiewicz 2009; Stuart and Lister 2011). It cannot be ruled out that this canine was imported either from North Africa or southwest Asia.

In Ukraine, *P. leo* has been reported mostly from the southern regions along the northern coast of the Black Sea (Table 1; Bibikova 1973; Vörös 1983; Krakhmalnaya 1999; Zhuravlev 1999; Daróczy-Szabó et al. 2020). The oldest

Ukrainian records of *P. l. persica* come from the settlement sites Bolhrad (6.4–6.0 kyr BP) and Molukhov Bugor (6.0–5.0 kyr BP) (Bibikova 1973; Vörös 1983). Bibikova (1973) described a lion phalanx from the settlement near Bolhrad dated as 6.4–6.0 kyr BP. From the Late Tripolye settlement near Maiaky, also in Odesa Oblast of Ukraine, she described nine bones of two individuals, one of which was a young animal. Bibikova (1973) emphasised that the landscape conditions near the mouths of the Dniester, Dnieper and Bug rivers in the early historical and ancient times were quite suitable for the habitation of this animal. Gromova (1928, 1932) reported a P4 from the site Olviya (Pontic Olbia) and Bibikova (1958) mentioned several additional specimens (archaeologically dated as 2.5–2.0 kyr BP) as belonging to three or four individuals. At the Berezan settlement, the lion was identified based on four teeth and a fragmentary upper jaw (Zhuravlev 1983a; Yanish and Kasparov 2015), the latter being reported as ‘intermediate’ between the lion and the leopard (Yanish and Kasparov 2015). Leopard remains are also known from southern Ukraine, where they were found in sediments of Eneolithic and Hellenistic times (Bibikova 1958; Kasparov and Sablin 2004). Some previous authors doubted that the Olbian lions were of local origin and suggested their being inhabitants of menageries (Gromova 1928; Bibikova 1958). However, taking into account all the available evidence, the lion occurrence in the Holocene of Ukraine can be considered proven.

The extant lion material has been reported from nine Ukrainian sites, but it is rather fragmentary or represents juvenile individuals or postcranial remains of low diagnostic value. Nevertheless, it corresponds metrically and morphologically to the Holocene lion finds from other European countries, e.g., Bulgaria (Ninov 1989, 1999) and Hungary (Vörös 1983, 1987). The Holocene lions of Europe, including those from Ukraine, do not seem to differ from the extant lion subspecies *P. l. persica*, the Persian lion. Therefore, we assign the Ukrainian Holocene lion remains to this subspecies *P. l. persica*. They include rather slender long bones and metapodials suggesting small and gracile lions (Fig. 8c). Among Hungarian and Bulgarian lions much larger and more robust individuals are known, like those from Tiszalúc and Gyöngyöshalász (Vörös 1983, 1987) or the mandible from Durankulak (Ninov 1989, 1999). As in the case of the Pleistocene *P. spelaea*, Persian lions also show considerable sexual size dimorphism in the cranial, dental, and postcranial elements (Gross 1992; Daróczy-Szabó et al. 2020). Therefore, the available postcrania from Ukraine can mostly represent females.

The body mass estimates are 82–88 kg for the Olviya lion (obviously a female) and 170–190 kg for the Mayaki specimens (males) (Table 4). These estimates are in accord with the data for smaller subspecies of the modern lion such as *P. l. senegalensis* (Meyer, 1826). For example, two lionesses from Waza National Park (Senegal) had a total length of 237 cm

and 240 cm, height of 81 cm and 80 cm, and mass of 103 kg and 110 kg (Fobuzie et al. 2007). Four other reported lionesses were 80, 87, 90 and 110 kg in weight (Bauer and Longh 2005; Longh et al. 2009). For lions from India, the data are as follows: total length 240–300 cm, head and body length 160–200 cm, shoulder height 90–110 cm, mass 160–200 kg, greatest skull length 330–367 mm for males; and total length 220–260 cm, mass 100–120 kg, greatest skull length 289–305 mm for females (Smee 1834; Fenton 1909; Cadell 1935; Pocock 1939; Wynter-Blyth and Dharmakumarsinhji 1950; Dharmakumarsinhji and Wynter-Blyth 1951; Nowell and Jackson 1996; Divyabhanusinh 2005). For the Persian lion, a male and a female skull had greatest length of 328 mm and 286 mm, respectively (Hemmer 1974). Mazák (2010) mentioned a skull from Iran with a length of 347.1 mm, and Heptner and Sludskii (1992: 93) stated that ‘In overall size the Persian lion corresponds to Central African animals’. Noack (1908) described one Iranian lion from Hagenbeck’s menagerie as a rather small, strongly built, yellowish male with a short, light mane.

Interestingly, the maxilla from Berezan holds traces of cutting with a small cleaver at the level of P2 (Yanish and Kasparov 2015). It is unclear for what purpose the skull was cut in such a manner. In this regard, it should be noted that remains of dogs with traces of undoubtedly culinary butchering have been found at Berezan (Zhuravlev 1983b). At the Chalcolithic site of Meshoko near Maikop, dated as 2.6–2.5 kyr BP, the distal part of the leopard humerus with traces of cutting has been reported (Kasparov and Sablin 2004). Large felines could be related to some rituals, such as the one conducted with the Aurignacian ivory figurine from Hohlenstein Stadel Cave in Germany (Conard 2003; Conard and Bolus 2003; Kind et al. 2014; Cueto et al. 2016). Upper Palaeolithic graphic expression places the lion in a prominent hierarchic position in the early humans’ symbolic world, giving these felids an important role in human culture

as a motif (Crémades and Laville 1995; Chauvet et al. 1995; Spassov and Stoychev 2005; Cueto et al. 2016). Activities such as the lion hunt that signifies the manhood rite of passage, as conducted by the Masaai people, connect the African lion with cultural symbolism (Hazzah et al. 2009).

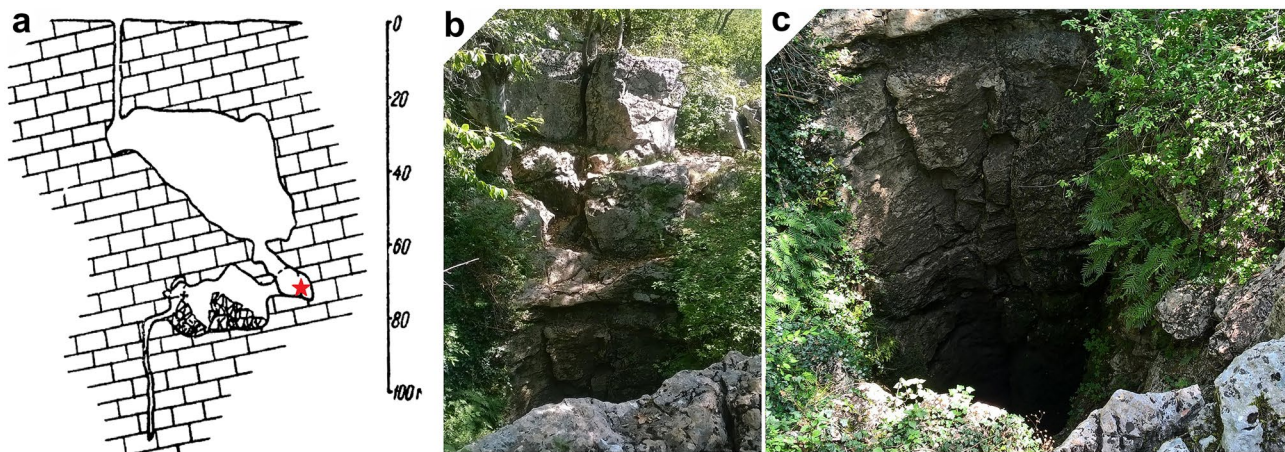
The Eurasian brown bear *Ursus arctos arctos* Linnaeus, 1758 and *P. l. persica* were the only Holocene predators in Ukraine that posed real, lethal danger to people and inspired awe throughout history. Their killing was often not for human protection but a courageous enterprise for hunters, a test of skills and strength (Hazzah et al. 2009; Daróczy-Szabó et al. 2020). Such interactions and related stories caused ancient hunters to treat lions as objects of worship and present their images in various forms, such as the manufactured zoomorphic borer from the Neolithic site Vovnig in Ukraine (Kovalchuk et al. 2018: fig. 3a-d). The artefact probably depicts a lion head and so may serve as indirect proof of the species presence in the region. This maneless lion would be a characteristic element of cave paintings and many Holocene artefacts, even though the maned lions dominated in the art of this period (Capitan et al. 1924; Friant 1940; Hemmer 1967; Spassov and Stoychev 2005; Masseti and Mazza 2013).

Establishing how long the Persian lion existed in Ukraine is difficult. The European records of *P. leo* are most common from the period when the abundance of wild herbivores was high (Vörös 1981, 1983; Daróczy-Szabó et al. 2020). Later, the combined effect of climate change and anthropogenic disturbance seems to have changed vegetation composition (Willis 1994, 1995; Magyari et al. 2010). The timing of this turnover varies with the region (Willis et al. 1998; Daróczy-Szabó et al. 2020). Locally, some areas could hold habitats with abundant potential prey (equids, bovids, antelopes, wild boars, and deer) and so remain favourable for the survival of large carnivorans.

**Fig. 9** Artistic depiction of Grand Prince Vladimir Monomakh’s encounter with a ‘fierce beast’, supposedly a Persian lion. It is loosely based on *The Instruction of Vladimir Monomakh* and the 11th-century frescoes of Saint Sophia Cathedral in Kyiv. Drawing by Velizar Simeonovski







**Fig. 10** Kryshtaleva Cave, or Maksimovich Cave, the locality of *P. s. spelaea* NMNHU-P OF-803/1964. It is a vertical karst cave in the Upper Jurassic limestones on the western slope of the Ai-Petri massif, Crimea (44°26'39"N, 33.°54'41"E). The lioness apparently fell into the entrance and later washed to the bottom of the hall (Bach-

ynsky and Dubliansky 1966; Bachynskiy 1970). **a.** cross section of the cave (after Bachynskiy and Dubliansky 1966: Fig. 1), red star indicates where the skeleton was found in 1964; **b-c.**, the entrance (photo by A. Trifonov, article 'Peshchera Maksimovicha' at <https://ru.wikipedia.org>)

There is no direct evidence for the presence of the Persian lion in medieval Ukraine, but some written sources suggest it was the case. The most famous is *The Instruction of Vladimir Monomakh* (ca. 1117) by Grand Prince of Kyiv Vladimir Vsevolodovich Monomakh. The text includes some hunting stories in his dominions of Chernihiv and Turov and an encounter with a 'fierce, shaggy animal', which sprang toward his thighs and injured him and his horse (Fig. 9). The 'fierce beast' in the Slavic translation of the Bible is a lion. Although this animal has been identified variously, e.g., as the Caspian tiger *Panthera tigris virgata* (Illiger, 1815) or Persian leopard *Panthera pardus tulliana* (Valenciennes, 1856), most commentators agree that it could be a lion (Miller 1877; Charlemagne 1964; Mavrodin 1964, 1965; Sapunov 1965; Heptner 1969; Larin 1977; Sumnikova 1986; Likhachev 1993; Savelyeva 1995; Stavisky 2009). According to the description, the animal jumped on the man and knocked him over with the horse. Even the largest leopards are too small to knock down a rider and a horse. Also, the 'beast' was described as very large and shaggy, which excludes the leopard (Fig. 9). As for the tiger, there is no evidence or any reference to this species in Slavic art, legend, or folklore, as opposed to the lion (Mayorov 2006). Of course, the occurrence of the lion in Slavic art, legend, and folklore cannot serve as reliable evidence for its presence in medieval Ukraine. Many Slavic toponyms are derived from the word 'lev', the Slavic for lion, and this may be an additional hint of the former occurrence of lions there. The name of the city of Lviv translates as 'the land of lions'. This association with lions might have been introduced by foreign influences. But of note is that lions in Ukrainian art are not overly stylised and look like made by people who had seen live animals. This is best

exemplified by the 11th-century frescoes of Saint Sophia Cathedral in Kyiv (Charlemagne 1964; Tsvelykh 2021).

## Conclusions

The presence of the cave lion *Panthera spelaea* has been recorded from 46 Ukrainian localities (36 caves sites and 10 open-air sites) dated from the early Middle to the Late Pleistocene, which covers the timespan between MIS 19–2, or 800–18/17 kyr BP. Two Middle Pleistocene localities, Siniakovo 1 and Sambir, document the occurrence of *P. s. fossilis*. The calcaneus and lower carnassial from Sambir represent an individual, comparable to the largest specimens of mid-Middle Pleistocene *P. s. fossilis* from Château, Mauer, Mosbach 2 and Południowa Cave. The material from three sites (Chernihiv, Bilykh Stin Cave and Kaniv) of uncertain age, possibly late Middle Pleistocene, was cautiously identified as *Panthera spelaea* ssp., although the Bilykh Stin lion is morphologically close to *P. s. intermedia*. The Ukrainian records of *P. s. spelaea* are dated to the Late Pleistocene or the latest Middle Pleistocene (MIS 6). A well-preserved skull of the *P. s. spelaea* from Kryshtaleva Cave was described and ASM-dated to 22.0–21.5 cal kyr BP. It is one of the smallest specimens of the cave lion ever found.

Analysis of the Ukrainian material of *P. spelaea* revealed the same trend of decreasing body size that is known from other Eurasian sites. The Middle Pleistocene subspecies *P. s. fossilis* is exemplified by the giant Sambir lion, while the late Middle Pleistocene specimens, still very large, are smaller than the predecessor. The Late Pleistocene individuals of *P. s. spelaea* are yet smaller, and among those from MIS 3–2 there are exceptionally small specimens, such as the dwarf lioness from Kryshtaleva Cave.



The history of lions in Ukraine is remarkable for including both *P. spelaea* and *P. leo*. The occurrence of the extant lion is known from nine sites in southeastern Ukraine archaeologically dated as 6.4–2.0 kyr BP. Some historical evidence suggests that the species might have survived in the region for a longer time. The published specimens are metrically and morphologically indistinguishable from the modern Persian lion *P. l. persica* and can be assigned to this subspecies.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10914-022-09635-3>.

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**Authors’ contribution** All authors have made substantial contributions to this submission. The individual contribution of each co-author is as follows: AM—conceptualisation, introduction, morphological and metrical studies, description of bones, morphological and metrical results, writing, Figs. 2, 3, 4, 5, 6, 7 and 10, and Tables 1, 2, 3, 4, Online Resource 1; DVI—resources, conceptualisation, metric and morphological results and discussion, writing; YAS—resources, information on sites, metric and morphological results and discussion, Figs. 1, 2, 3; ST—the radiocarbon date, conceptualisation, writing, investigation, resources; BR—conceptualisation, writing, investigation, resources, description of sites and the material, metric and morphological results and discussion, Figs. 1, 10, 3, 4; AV—description of sites and material, metric and morphological results and discussion; YY—investigation, resources, description of sites and the material; OK—investigation, resources, description of sites and the material, metric and morphological results and discussion.

**Data availability** All data analysed and discussed in the study are included in this article and its supplementary information file (Online Resource 1).

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