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Morphometric comparison of *Panthera spelaea* (Goldfuss, 1810) from Poland with the lion remains from Eurasia over the last 700 ka

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ABSTRACT

The Pleistocene lion *Panthera spelaea* was not a homogenous taxon; it was represented by three chronoforms. The oldest one, from the Early and Middle Pleistocene, was *P. s. fossilis*, the youngest was the Late Pleistocene cave lion *P. s. spelaea*. The intermediate form between them was *P. s. intermedia*. The scarcity of stratigraphically old lion made it difficult to understand the evolution of this carnivore. Therefore, we revised the fossil material of the Pleistocene lion from Polish excavation sites. The analysis revealed the presence of *P. s. fossilis* in 7 sites: Tunel Wielki, Południowa, Wschodnia, Draby, Biśnik, Deszczowa and Wierzchowska Górna caves. The remains from these localities significantly differed in their average size and teeth proportions from the nominate younger chronoform, i.e. the cave lion. Using this material and all other available data, we compared the lion remains grouped into four palaeoclimate periods: MIS 17-12, MIS 11-9, MIS 8-6 and MIS 5-2. We found significant time-related trends in many morphometric features of dentition and limb bones. Between the first two periods, the lion became larger but from MIS 8, it gradually decreased in size. The teeth showed a much greater rate of changes than the metapodial bones, which in turn were characterised by more heterogeneous and mosaic evolution. The changes observed in the fossil material can result from *in situ* evolution of lion populations occupying Europe or immigration and replacement of the native forms by those from other regions, for example Asia.

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1. Introduction

The lion constituted an important component of the Pleistocene ecosystem in Eurasia as a main carnivore since the late Pleistocene to the Early Holocene, when it became extinct about 13 ka (Stuart and Lister, 2011). Three forms of the Pleistocene ranked as chronosubspecies (Barycka, 2008; Argant, 2010b; Marciszak and Stefaniak, 2010; Marciszak et al., 2014) or sibling species (Sotnikova and Nikolskiy, 2006; Hankó, 2007; Sabol, 2011b) are commonly recognised.

The oldest known remains of the lion assigned to *P. s. fossilis* (von Reichenau, 1906) were described from the late Early Pleistocene (1200-800 ka) of Western Siberia (Sotnikova and Foronova, 2014) and Moldova (David, 1980, 1999). However, their stratigraphical and taxonomical positions are debatable (Foronova, 2001; Hemmer, 2011; Sotnikova and Foronova, 2014). In Europe, the oldest accepted records are dated as 750-680 ka and come from Pakefield in Great Britain (Lewis et al., 2010). The oldest find from continental Europe is dated as 700-650 ka (Sala, 1990). The

Abbreviations: **C**, caudal vertebra; **L**, lumbar vertebra; **mtcp**, metacarpal bone; **mtts**, metatarsal bone; **ph I-1(2/3/4/5)-a**, first (second/third/fourth/fifth) proximal phalanx of manus; **ph I-2(3/4/5)-p**, second (third/fourth/fifth) proximal phalanx of pes; **ph II-1(2/3/4/5)-a**, first (second/third/fourth/fifth) medial phalanx of manus; **ph II-2(3/4/5)-a**, second (third/fourth/fifth) medial phalanx of pes; **ph III**, distal phalanx; **T**, thoracic vertebra.

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presence of this great lion is documented from 62 Eurasian sites dated between 1200 and 300 ka (Fig. 1, Table 1).

Table 1. Occurrence of *P. s. fossilis* in the Pleistocene of Eurasia. Locality numbers (Map) correspond to those in Fig. 1.

The second form of lion, called *P. s. intermedia* Argant and Brugal (2017), was recently described based on the abundant fossil material from the French site Igue-des-Rameaux dated as MIS 10/9-7 (Argant and Brugal, 2017). Similar lion remains with "intermediate" features between the Middle and Late Pleistocene lions were also described from other European localities dated as 350-150 ka (Hemmer, 1974, 2011; Schütt and Hemmer, 1978; Argant et al., 2007; Argant, 2010a,b; Marciszak and Stefaniak, 2010; Marciszak et al., 2014). The third, stratigraphically youngest form, is called *P. s. spelaea* and its oldest occurrence in Europe is dated as 200-180 ka (Marciszak and Stefaniak, 2010; Hemmer and Keller, 2011; Sabol, 2011a,b; 2014).

Compared to *P. s. spelaea*, *P. s. fossilis* had smaller incisors, less flattened and comparatively narrower canines, broader P3 with shorter and higher paracon, less reduced additional cusplets (protocon and hypocon) and more strongly developed posterior cingulum; broader P4, buccally and lingually much broadened in its middle part, with broad and high protocon but small and low parastyl, its paracon was higher and longer than the metacon; large and broad p3 with high and long protoconid; proportionally longer and wider p4 with shorter and higher protoconid; oval and robust m1 usually slightly shorter than p4, with well-developed main cusps, its paraconid and the protoconid were rather equal in height and length, it also showed the zigzag enamel structure and median, lingual bulge (Kurtén, 1960, 1968; Dietrich, 1968; Schütt, 1969a; Hemmer and Schütt, 1970; Ballesio, 1975; Schütt and Hemmer, 1978; Erdbrink, 1983; Argant, 1988, 2000, 1991; Guzvica, 1998; Baryshnikov and Boeskorov, 2001; Groiß, 2002; Hemmer, 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). *P. s. intermedia* differed from *P. s. fossilis* in its smaller size, less massive muscle attachments, triangular and shorter mandible ramus with shallower and shorter masseteric fossa, narrower canines, narrower P4 with almost straight buccal margin, narrower and smaller m1 with less developed bulge and zigzag enamel, as well as more gracile metapodials and calcaneus (Argant and Brugal, 2017).

Many Pleistocene lion remains have been described from cave and open sites in Poland since almost 200 years ago (Kowalski, 1959; Barycka, 2008; Marciszak et al., 2019). Two lion forms were reported already in 1906 (von Reichenau, 1906), however, so far only one chronoform from Poland was recognised as a cave lion. Only Barycka (2008) as well as Marciszak and Stefaniak (2010) made a detailed analysis showing the presence of a stratigraphically older lion in the Polish fauna. According to Barycka (2008), *P. s. fossilis* remains were preserved in caves Wierzchowska Górna and Deszczowa, while Marciszak and Stefaniak (2010) reported this form from Biśnik cave. However, so far no complete revision of the whole Polish material of the Middle Pleistocene lion has been done.

The re-discovery and revision of some old collections in Kraków, Warsaw and Wrocław museums, as well as new excavations, provided new Middle Pleistocene lion material from Poland. A preliminary survey showed that this lion differed morphometrically

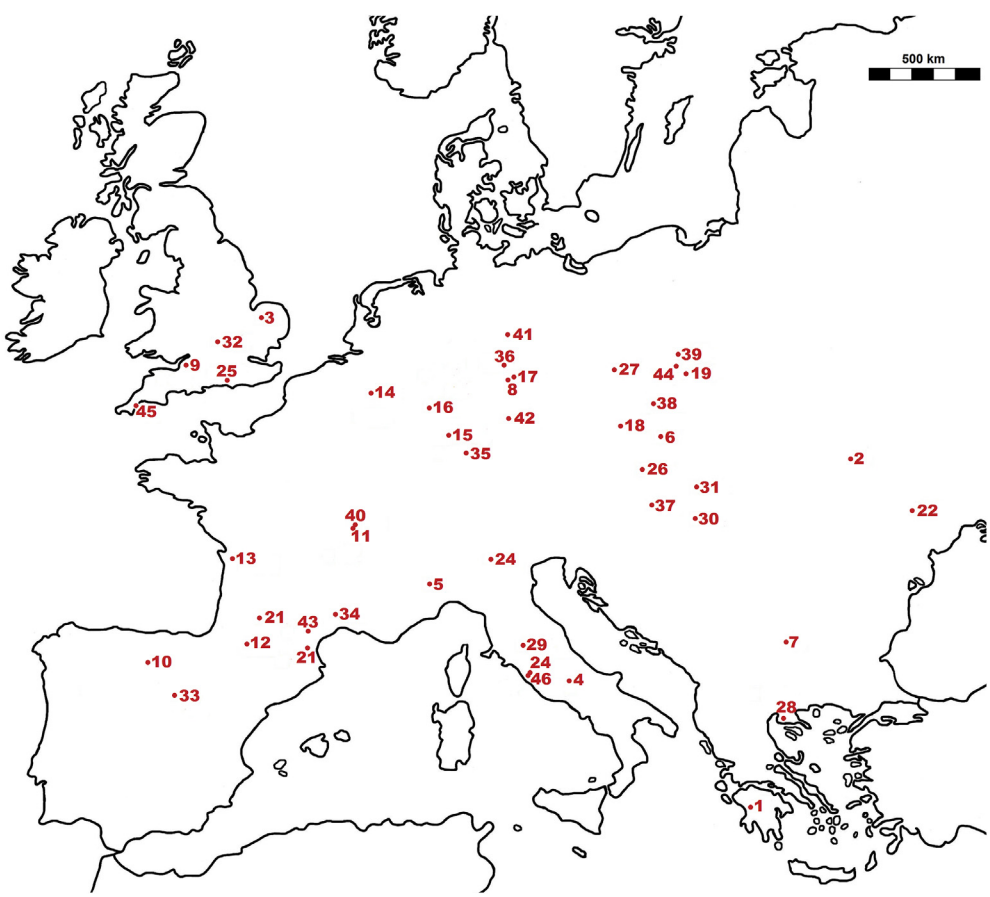

Fig. 1. Distribution of Pleistocene sites with *P. s. fossilis* in Europe. For locality numbers see Table 1.

Table 1
Occurrence of *Panthera spelaea fossilis* in the Pleistocene of Eurasia. The numbers of particular localities (Map) correspond to those presented in Fig. 1.

Map	Site	Age (MIS)	References
1	Megalopolis-Marathousa	31-29?	Sickenberg (1976)
	Bachatsk	23-22?	Foronova (2001); Sotnikova and Foronova (2014)
2	Sinjakovo 1	20-17?	David (1980), 1999
3	West Runton	17	Turner (2009); Lewis et al. (2010)
3	Cromer Beach	18–17	Turner (2009); Lewis et al. (2010)
3	Pakefield	19	Freudenberg (1914); Turner (2009); Lewis et al. (2010)
4	Isernia la Pineta	17–16	Sala (1990)
5	Valdemino cave	16–15	
6	Koněprusy C 718	16–15	Argant et al. (2007)
7	Kunino	16–15	Kahlke et al. (2011)
8	Süßenborn	16–15	Hemmer and Schütt (1970)
9	Westbury-sub-Mendip	15	Bishop (1982); Turner (1999), 2009
10	Trinchera Galeria	15–13	Cervera (1992); Garcia (2003)
11	Château Breccia	15–13	Argant (1991), 2000; Argant et al. (2007), 2008
12	Montmaurin	15–13	Saint-Perrier, 1922
13	Artenac cave	15–13	Tournepiche (1996)
14	La Belle-Roche	15–13	Cordy (1995); Kleczko (1999)
15	Frankenbacher Schotter	15–13	Döppes and Rosedahl (2008)
15	Mauer	15–13	Wurm (1912); Kurtén (1960); Dietrich (1968); Hemmer (1974); Marciszak et al. (2014)
16	Mosbach 2	15–13	von Reichenau, 1906; Dietrich (1968); Schütt (1969a); Hemmer and Schütt (1970); Hemmer (1974)
17	Urd cave	15–13	Feustel et al. (1971)
18	Stránská Skála	15–13	Stehlik, 1934; Thenius (1972)
19	Tunel Wielki cave	15–13	this work
20	Grotte XIV	14–13	Langlois (2002)
21	Arago cave	14–12	Crégut (1979); Testu (2006)
22	Kolkotova Balka	14–12	David (1980), 1999
23	Soave Monte Tenda	13–12	Bona and Sardella (2012)
24	Rome-Ponte Molle 1	13–12	Pasa (1947); Petronio et al. (2011)
25	Boxgrove	13	Parfitt (1999)
10	Sima de los Huesos	13	García et al. (1997); García and Arsuaga (2001); Garcia (2003)
26	Deutsch Altenburg 1	13–12	Freudenberg (1914); Nagel and Rabeder (1997)
27	Południowa cave	15–12	this work
23	Soave Castello	13–12	Bona and Sardella (2012)
23	Soave Sentiero	13–12	Bona and Sardella (2012)
23	Soave Viatelle	13–12	Bona and Sardella (2012)
23	Cerè cave (cf.)	13–12	Ghezzo et al. (2014)
28	Petralona cave	15–12	Hemmer (1974); Kurtén and Poulianos (1977), 1981
29	Fontana Ranuccio	12	Palombo and Mussi (2006)
30	Somssichhegy 2	12–11	Hankó (2007)
31	Kövesvárad	12–11	Jánossy (1969); Hankó (2007)
32	Swanscombe	11	Sutcliffe (1964); Turner (1997)
33	Toralba Ambrona	11	Soto et al. (2001)
34	Lunel Viel	11	Bonifay (1971)
35	Heppenloch	11	Adam (1975)
36	Bilzingsleben	11	Toepfer (1983); Turner (1997)
37	Vertesszöllös 2	11	Jánossy (1969); Antón et al. (2005); Hankó (2007)
38	Žernavá	11	Musil (1969)
39	Draby 3 and 5	11	this work
40	Azé cave	11	Argant (1988); Sotnikova and Nikolskyi, 2006; Argant and Brugal (2017)
41	Unicorn cave	12–10	Schütt (1969a); Hemmer and Schütt (1970);Nowakowski and Stefaniak, 2015 Hemmer (1974)
42	Moggaster cave	12–10	Groiss (1992)
43	Aldene	11–10	Testu (2006)
10	Trinchera Dolina	11–10	Aguirre et al. (1990); Garcia (2003); Blasco et al. (2010)
44	Biśnik cave, layers 19ad-19	10–9	Marciszak and Stefaniak (2010)
37	Varhegy	11–10	Jánossy (1969); Hemmer and Schütt (1970); Hankó (2007)
38	Za Hajovnou cave	11–9	Ábelová (2005); Sabol (2014)
19	Wierzchowska Góra cave	10–9	Barycka (2008)
45	Kent's cavern (breccia)	9	Proctor et al. (2005)
46	Torre in Pietra	9	Caloi and Palombo (1978)
27	Wschodnia cave	?	this work

from *P. s. spelaea* from the Late Pleistocene sites (Marciszak and Stefaniak, 2010; Marciszak et al., 2014). The analyses demonstrated also certain morphological changes in the dental characters of the Polish Pleistocene lion during the middle Middle and the late Middle Pleistocene. These finds are of great importance for understanding of the Pleistocene lion evolution through geological time because the European material of the Middle Pleistocene lion is generally very scarce. Therefore, the aim of this study was description and revision of this material as well as its inclusion in a comprehensive analysis of all available Eurasian lion remains dated from MIS 17 to 2. The studied period covers over 700 ka.

2. Material

All original material analysed in this paper was examined by the authors. The material from caves Tunel Wielki, Deszczowa and Wierzchowska Górna is stored at the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences in Kraków. The material from caves Biśnik, Draby 8, Południowa and Wschodnia is kept at the Department of Paleozoology, University of Wrocław. The

material from Draby 5 is stored at the Institute of Paleobiology, Polish Academy of Sciences in Warsaw. The list of the studied material is presented in Table S1 (Appendix 2). A more detailed description of sites, together with their fauna associated with *P. s. fossilis*, is given in Chapter 1.1 of Appendix 1.

The morphometric analysis was based on our own measurements as well as those taken from the literature (Dawkins and Sandford, 1866; Filhol and Filhol, 1871; Boule, 1906; von Reichenau, 1906; Freudenberg, 1914; Edinger, 1931; Riabinin, 1932; Lubicz-Niezabitowski, 1938; Mottl, 1949; Pidoplichko, 1956; Kabitzsch, 1960; Malez, 1963; Rakovec, 1964; Terzea, 1965; Zapfe, 1966; Samson and Kovacs, 1967; Dietrich, 1968; Schütt, 1969a, 1969b; Suire, 1970; Vereshchagin, 1971; Thenius, 1972; Hemmer, 1974; Adam, 1975; Ballesio, 1975; Daxner-Höck, 1975; Hemmer, 1977; Kurtén and Poulianos, 1977; Caloi and Palombo, 1978; Schütt and Hemmer, 1978; Crégut, 1979; Ballesio, 1980; Clot, 1980; Clot et al., 1980; Altuna, 1981; Kurtén and Poulianos, 1981; Bishop, 1982; Riedel, 1982; Turner, 1982; Edbrink, 1983; Toepfer, 1983; Nielbock, 1987; Ruprecht, 1987; Argant, 1988; Dufour, 1989; Alekseeva, 1990; Kretzoi, 1990; Sala, 1990; Argant, 1991; Cervera, 1992; Groiss, 1992; Gross, 1992; Fischer, 1994; Valensi, 1994; Turner, 1997; Guzvica, 1998; Kleczko, 1999; Turner, 1999; Baryshnikov and Boeskorov, 2001; Foronova, 2001; Groiß, 2002; Garcia, 2003; Ábelová, 2005; Bona, 2006; Sotnikova and Nikolskiy, 2006; Testu, 2006; Argant et al., 2007; Diedrich, 2007; Hanko, 2007; Toškan, 2007; Barycka, 2008; Baryshnikov and Petrova, 2008; Ovodov and Zaika, 2008; Döppes and Kempe, 2009; Argant, 2010a; Baryshnikov and Tsoukala, 2010; Lewis et al., 2010; Baryshnikov, 2011; Diedrich, 2011; Hemmer and Keller, 2011; Pautret-Homerville et al., 2011; Sabol, 2011a; Diedrich, 2012; Diedrich and Rathgeber, 2012; Marciszak et al., 2014; Sabol, 2014; Sotnikova and Foronova, 2014; Argant and Brugal, 2017).

3. Methods

3.1. Measurements

The identification of lion remains and their classification to individual forms were based on the classic morphometric analysis. Measurements were taken point to point, with an electronic calliper, up to the nearest 0.1 mm. Each value given in this paper is the mean of three measurements. The mean is rounded to one decimal place. All the measurements are expressed in mm. The scheme of measurements and morphological terminology follow Schmid (1940) and Argant (2010a) and are shown in Figs. S1–S3 in Chapter 1.2 of Appendix no 1. The measurements of cranial and postcranial elements are given in Tables S2–S13 (in Appendix 2). Throughout the text, the upper teeth are represented by capital letters (e.g. P4) and the lower ones as lowercase letters (e.g. p4).

3.2. Statistical analyses

Statistical tests were carried out only on data sets including at least three teeth and bone samples as well as indices as variables. In order to check if the analysed variables fit the normal distribution, we applied the Shapiro-Wilk test. The homogeneity of variance across the analysed groups was verified using the Lévene test. Two groups were compared using the unpaired t-Student test, when the assumption on the normality of distribution was fulfilled. Otherwise, its non-parametric counterpart, i.e. the unpaired Wilcoxon-Mann-Whitney test, was used to compare two groups. In the comparison of more than two groups, we applied the parametric one-way Analysis of Variance (ANOVA) with moderately conserved Tukey HSD post-hoc test, when the assumptions about normality of distribution and variance homogeneity were fulfilled. When at least one of these assumptions was violated, we used the non-parametric counterpart of ANOVA, Kruskal-Wallis test with Dunn's post-hoc test in pairwise comparisons between groups. In this post-hoc test and when many hypotheses were tested, we applied the Benjamini-Hochberg method for p-value correction to control the false discovery rate. Differences between the compared groups were considered significant when p-value was smaller than 0.05 but levels lower than 0.01 and 0.001 were also indicated. Spearman's correlation coefficient and their significance were calculated for particular teeth and bone measurements or indices ordered according to the stratigraphic classification of the remains. The percentage difference in the median of each variable between chronologically consecutive lion groups was calculated according to the formula: $D = 100\% \cdot (M_2\text{-}M_1)/M_1$, where M_2 and M_1 are median of a given variable (i.e. a measurement or an index) for a younger and an older lion group, respectively.

Statistical analyses were performed with R package 3.5.1 (A language and environment for statistical computing, R Core Team, 2018, R Foundation for Statistical Computing, Vienna, Austria). In the statistical analyses, the lion remains were classified into four groups representing the main evolutionary phases. The groups were assigned to Marine Isotope Stages (MIS). Using the newly described and identified *P. s. fossilis* remains as well as all available remains presented in the literature, we decided to analyse changes in the remains of lion over a wide range of time. Therefore, we classified the available material into four groups according to their palaeoclimatic age: MIS 17-12 (712-424 ka), MIS 11-9 (424-300 ka), MIS 8-6 (300-130 ka) and MIS 5-2 (130-14 ka). The first three groups correspond to the Middle Pleistocene and the latter to the Late Pleistocene. The classification of the lion remains into the four, quite extensive, time periods minimized the risk of their imprecise or wrong dating. The stratigraphic age of each lion remain was carefully checked and the sites with mixed faunas or those with no or imprecise dating were not included in the study.

4. Results

4.1. Detailed statistical comparison of Pleistocene lion groups over geological time

The morphometric differences between *P. s. fossilis* and *P. s. spelaea* were previously studied and summarised by many authors, e.g. by Kurtén (1960), Dietrich (1968), Schütt (1969a), Schütt and Hemmer (1978), Argant (1988, 1991), Sotnikova and Nikolsky (2006), Hankó (2007), Barycka (2008), Sabol (2014). These analyses were almost exclusively based on cranial and dental characters. Some researchers tried to include also mandibular features, especially when the lack of teeth excluded the typical dental analysis (Dietrich, 1968; Barycka, 2008; Sotnikova and Foronova, 2014). However, these features represent probably an intraspecific variation and cannot be used to distinguish the lion forms. These features are sexually dimorphic and ontogenetically highly variable, so their taxonomic usefulness is rather poor (Fig. 2, Table S5).

In this study, we included many morphometric characters not only of dentition, but also of limb bones. Based on these features, we revised the Pleistocene lion remains from Polish excavation sites (see Figs. 2–5 for pictures of these specimens and Chapter 1.3 of Appendix 1 for their description). Including these original data and those collected from the literature, we compared statistically the lion remains from MIS 17-2. The basic statistical parameters for stratigraphical groups of lions and all measurement types are shown in Table S14 and are presented graphically in box-plots in Fig. S4. In Figs. 6–9, we selected the most representative box-plots for variables showing statistically significant differences between

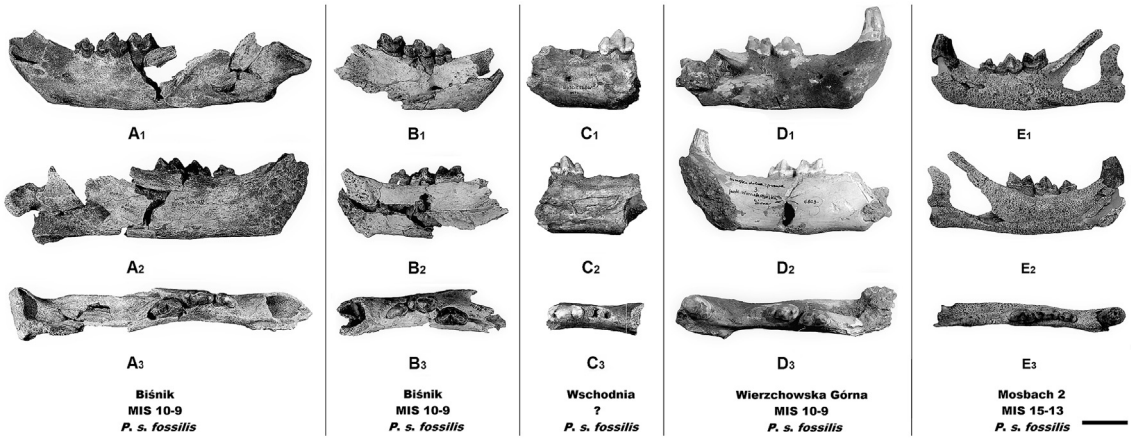

Fig. 2. Mandibles of *P. s. fossilis* from German and Polish Middle Pleistocene sites. All specimens are shown in the same scale; scale bar equals 50 mm; 1 - buccal view, 2 - lingual view, 3 - occlusal view.

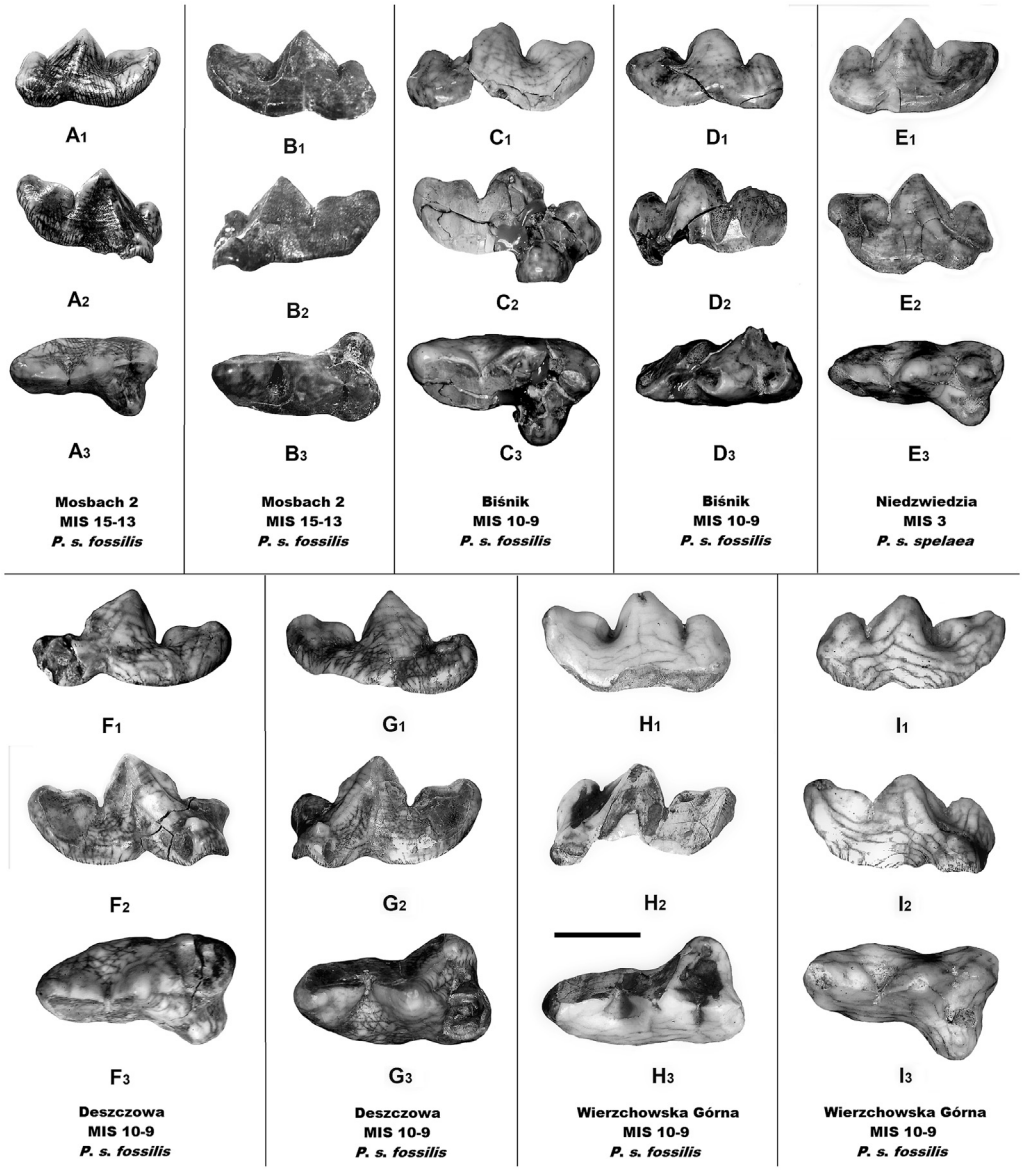

Fig. 3. Premolar teeth of *P. spelaea* from German and Polish sites. All teeth are shown in the same scale; scale bar equals 10 mm, 1- buccal view, 2 - lingual view, 3 - occlusal view.

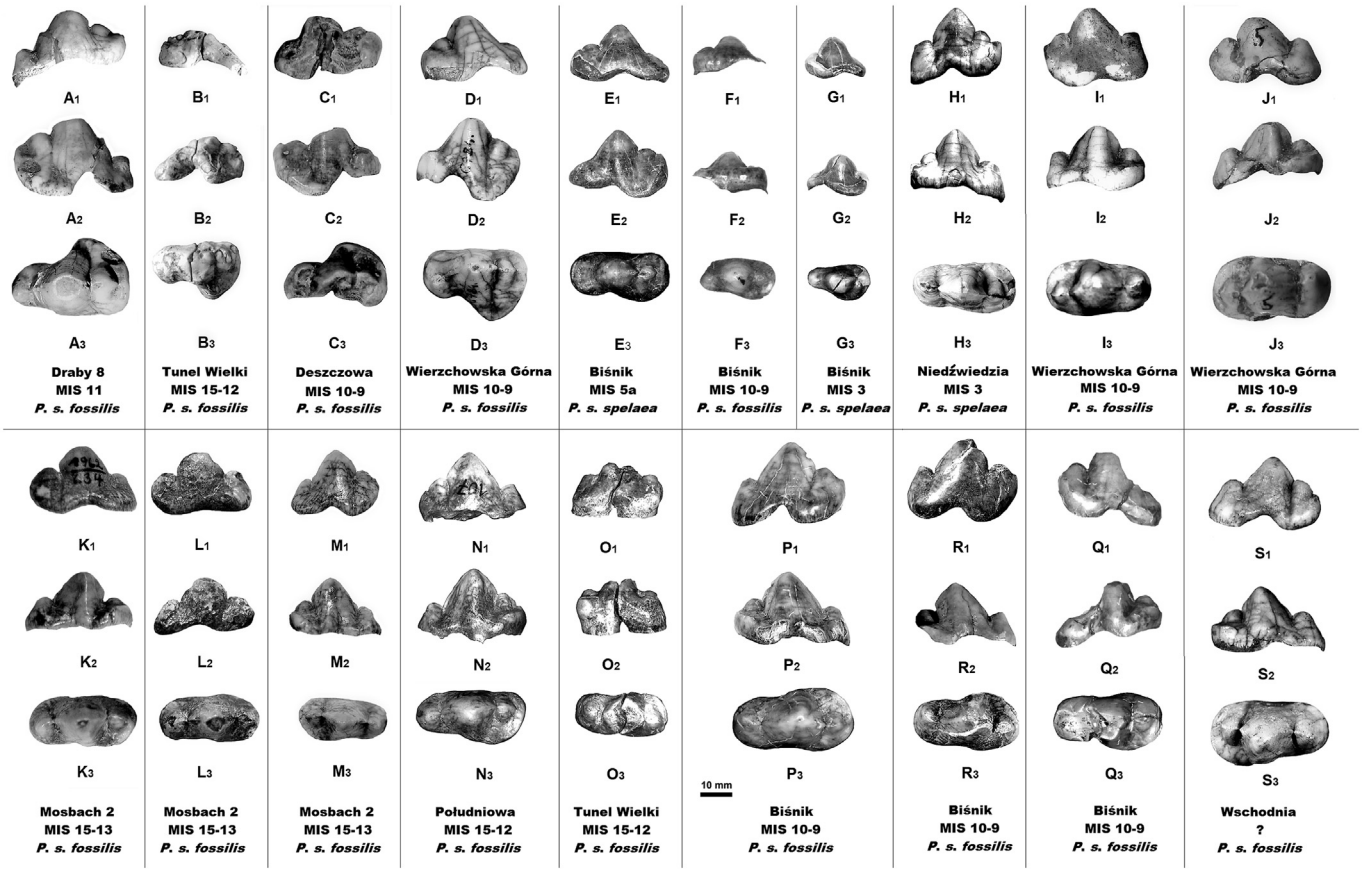

Fig. 4. P4 of *P. spelaea* from German and Polish sites. All teeth are shown in the same scale; scale bar equals 20 mm, 1 - buccal view, 2 - lingual view, 3 - occlusal view.

the lion groups. Table S15 contains all significant comparisons between these groups for the individual variables. In the description below, we focused on variables for which intergroup differences were supported by statistical tests.

We tested the concept that *Panthera spelaea* changed in the morphometric features of teeth and limb bones over the last 700 ka in four specified time periods. The null hypothesis was that there were no differences between the lions in these periods and the alternative that some differences existed. Moreover, we checked if the changes occurred with the same or different rate depending on individual measurement types and the remaining types (dentition vs. limb bones).

Comparing the data, we could recognise several morphometrical trends over time. One set of variables showed a steady or progressive increase from the chronologically oldest to the youngest samples (Figs. 3–4 and Fig. 6). Such trends are represented by indices for premolars: P3 (anterior to posterior breadth, Ba/Bp) (Fig. 4A–E and Fig. 6), P4 (metastyl length to the crown total length or paracon length, Lms/L and Lms/Lpa) (Figs. 3 and 6) and p4 (protoconid length to the crown total length, Lpr/L) (Fig. 4H–S and Fig. 6). For all of them, there are significant differences between the oldest (MIS 17-12) and the youngest (MIS 5-2) groups. For the P4 and p4 indices, there is also a significant difference between the MIS 11-9 and MIS 5-2 groups, while for the two P4 indices, the differences between MIS 8-6 and MIS 5-2 groups, as well as between MIS 17-12 and MIS 8-6 groups, are statistically significant (Figs. 3 and 6).

Many more measurements and indices show an opposite trend, i.e. a gradual decrease from the Middle Pleistocene to the most recent lion group (Fig. 7). The latter group differs significantly from all the others in p4 protoconid height (Hpr) (Fig. 4H–S), m1 paraconid length (Lpa) and the crown breadth to length ratio (B/L) (Fig. 5) as well as in the total length (L) of metatarsus III (Fig. 7). The lions from the MIS 5-2 group are also significantly smaller than those from the MIS 11-9 and MIS 8-6 groups in p4 paraconid height to the crown total length ratio (Hpr/L) (Fig. 4H–S and Fig. 7). They also differ from the MIS 17-12 and 8-6 groups in m1 paraconid length ratio to the crown total length (Lpa/L) and in the ratio of the crown total length of p4 to m1 (Lp4/Lm1). Moreover, the recent lions differ from the two oldest lion groups in the index breadth to length ratio (B/L) of canine, anterior breadth to the crown total length ratio (Ba/L) of p4, protoconid length (Lpr), m1 incisor height (Hin) and its ratio to the crown total length (Hin/L) as well as the maximal anteroposterior diameter (L) of talus (Fig. 7). Furthermore, the geologically youngest lions are smaller than: (a) the MIS 17-12 lions in protoconid length to the crown total length rato (Lpr/L) of m1, transverse diameter (B) and its ratio to anteroposterior diameter (B/L) of talus, (b) the MIS 11-9 lions in the minimal transverse middleshaft diameter (mB) of metatarsus II, and (c) the MIS 8-6 lions in paraconid height (Hpa) of m1, the maximal transverse diameter of distal epiphysis (dB) of metatarsus III, and the total length (L) of metatarsus IV as well as metacarpus III and IV. We also found significant differences between the lion remains dated as MIS 8-6 and those dated as MIS 17-12 and 11-9 in the breadth to length ratio (B/L) for canine and m1. The MIS 8-6 group is smaller than the MIS 17-12 group also with respect to the B/L index (the maximal transverse to vertical diameters) calculated for talus, while MIS 11-9 lions have smaller paraconid length to the crown total length ratio (Lpa/L) of m1 than the MIS 17-12 group (Fig. 7).

The general decreasing trend and smaller values for the

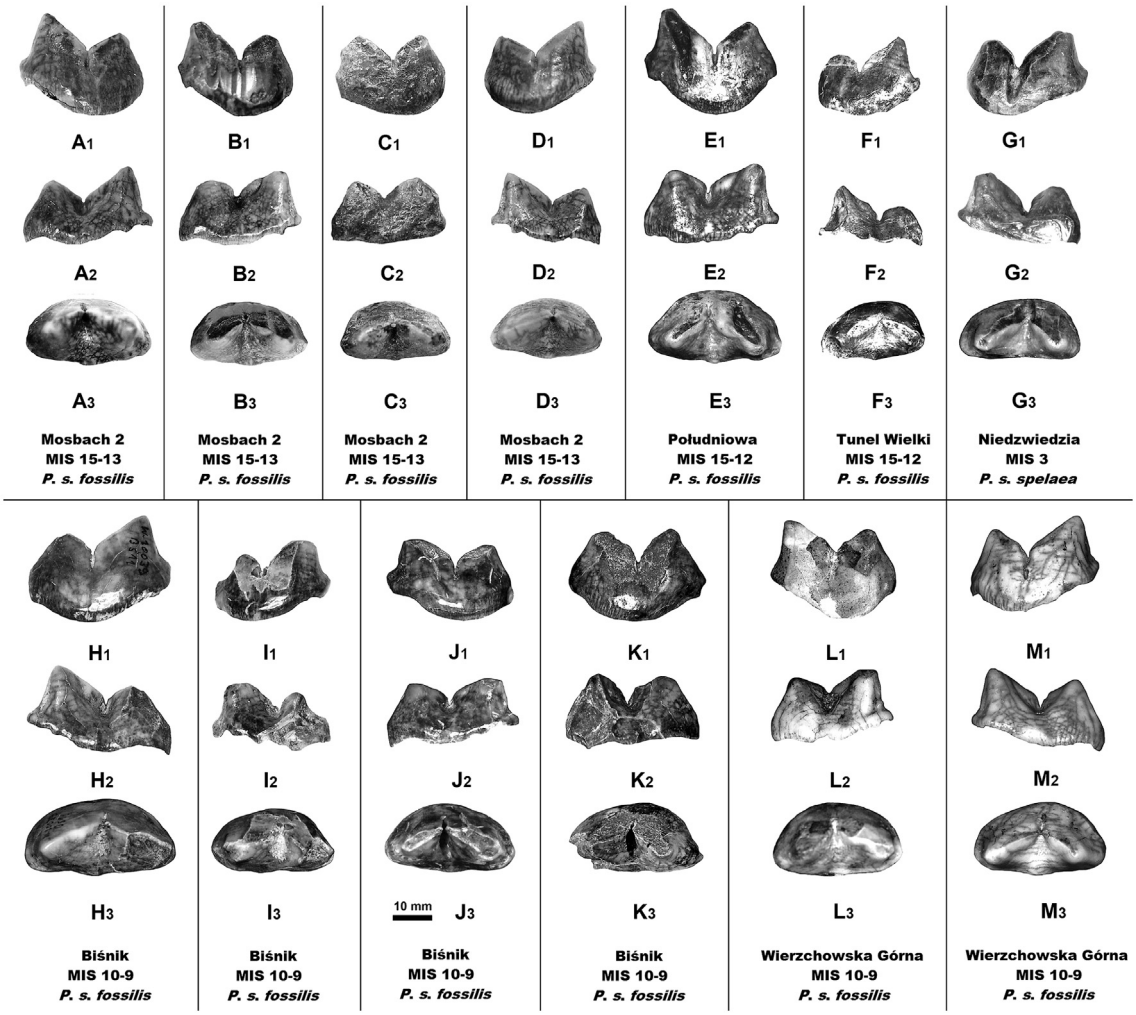

Fig. 5. Lower molar (m1) of *P. spelaea* from German and Polish sites. All teeth are shown in the same scale; scale bar equals 10 mm, 1 - buccal view, 2 - lingual view, 3 - occlusal view.

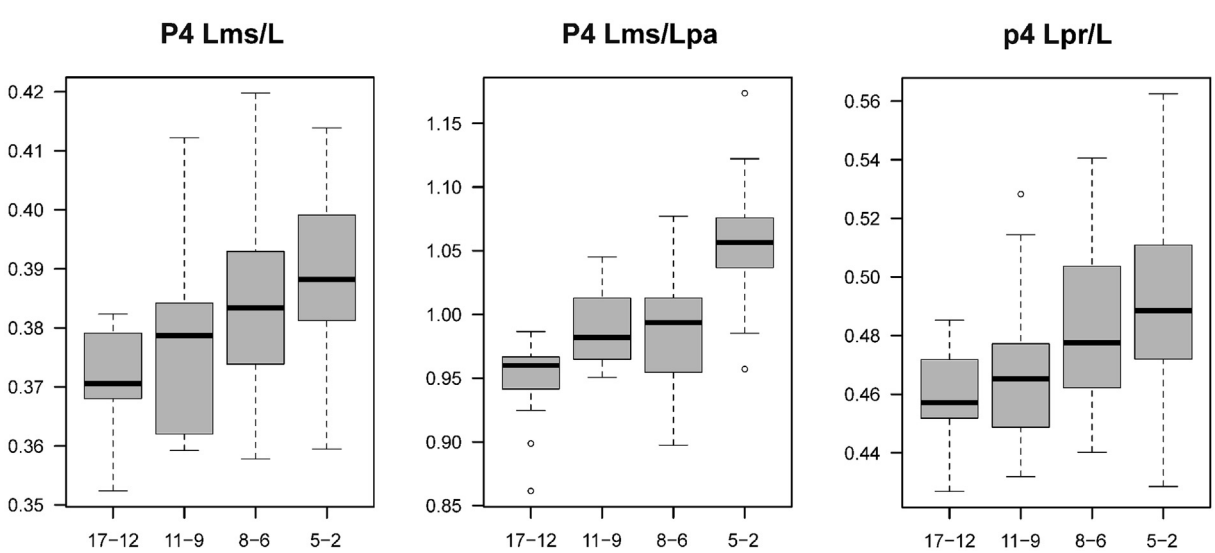

Fig. 6. Box-plots of selected measurement types of Pleistocene lion remains showing a steady or progressive increase from the geologically oldest to the youngest samples. The remains were clustered into four groups according to their palaeoclimatic age: MIS (Marine isotope stage) 17-12, 11-9, 8-6 and 5-2. The thick line indicates median, the grey box shows quartile range and the whiskers denote the range without outliers.

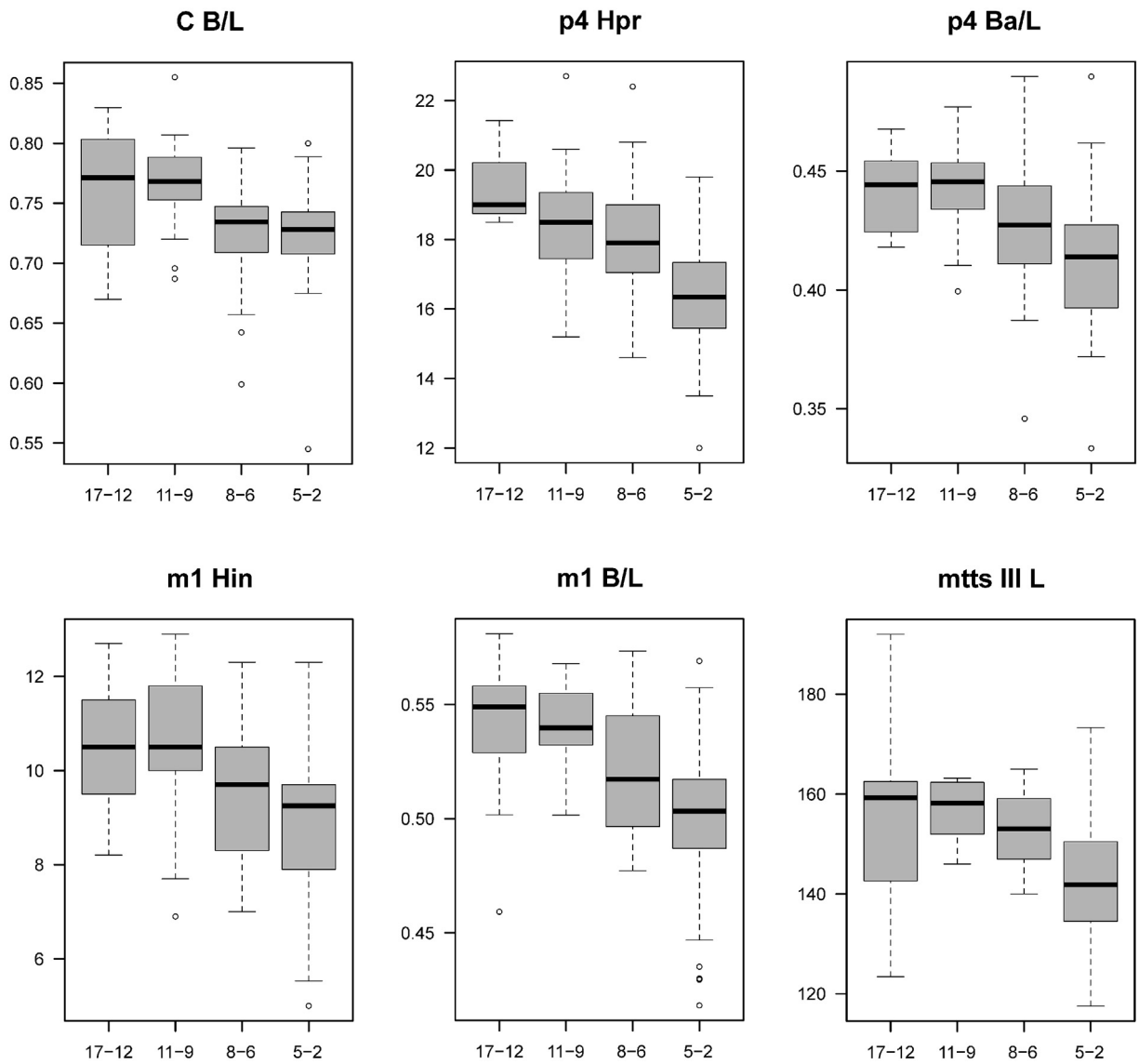

Fig. 7. Box-plots of selected measurement types of Pleistocene lion remains showing a steady or progressive decrease from the geologically oldest to the youngest samples. For other explanation see Fig. 6.

chronologically youngest lions can be also observed for other measurements and indices, e.g. paracon height (Hpa) of P3, total length (L) of metatarsus IV and V, maximal anteroposterior diameter of distal epiphysis (dL) of metatarsus V, maximal transverse diameter of distal epiphysis (dB) of metacarpus IV, but the differences between the groups are not supported by statistical tests (Fig. S4). We also noticed relatively large values for the oldest group in comparison to the others in the minimal transverse middle shaft diameter to the total length ratio (mB/L) of metatarsus II, the maximal anteroposterior diameter of proximal epiphysis (pL) of metatarsus III, P3 paracon height to the crown total length ratio (Hpa/L) and p4 protoconid height to the crown total length ratio (Hpr/L) (Fig. S4). However, the differences were not statistically significant either.

The other set of variables shows a decreasing tendency but only from MIS 11-9 to the two younger groups, since the geologically oldest group is characterised by smaller values than their predecessors dated as MIS 11-9 (Fig. 8). In consequence, the MIS 11-9 lions show the largest measurements and indices of all the groups. The differences between the remains dated as MIS 17-12 and MIS 11-9 are statistically significant for the measurements of P4 (Fig. 3): anterior (Ba) and posterior (Bp) breadth, paracon height (Hpa), crown total length (L), metastyl length (Lms); P3 (Fig. 4A–E): crown total length (L), anterior breadth (Ba), paracon length (Lpa); p3 (Fig. 4F–G): anterior (Ba) and posterior (Bp) breadth, and p4 (Fig. 4H–S): crown total length (L) and protoconid length (Lpr). The MIS 11-9 lion remains are also significantly larger from those from the next period (MIS 8-6) in their crown breadth (B) of canine and m1 (Fig. 5), anterior (Ba) and posterior (Bp) breadth of P4 (Fig. 3), p3 and p4 (Fig. 4), crown total length (L) of canine, P4, p3 and p4 (Fig. 4), protoconid length (Lpr) of p4 (Fig. 4H–S), anterior breadth to the crown total length (Ba/L) of P4 (Fig. 3), posterior breadth to crown total length ratio (Bp/L) of P4, p3 and p4 (Figs. 3 and 4), maximal anteroposterior diameter of distal (dL) and proximal epiphysis (pL) of metacarpus III, maximal anteroposterior diameter of proximal epiphysis (pL) of metacarpus V, minimal transverse middle shaft diameter (mB) and its ratio to the total length (mB/L) of metatarsus V as well as maximal anteroposterior diameter (L) of calcaneus and total length (L) of metacarpus V. The decreasing trend over time is maintained by the lion remains dated as MIS 5-2,

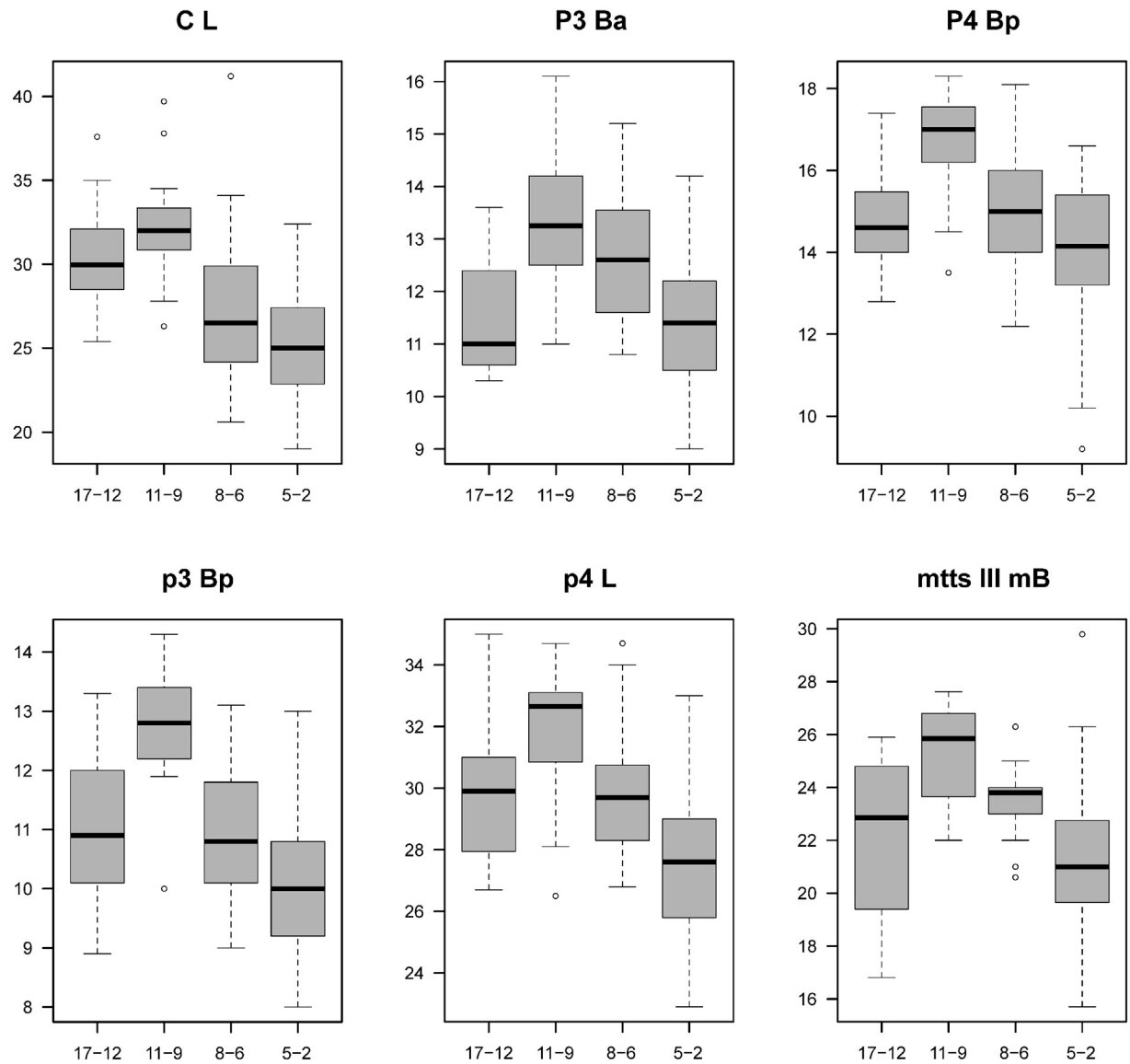

Fig. 8. Box-plots of selected measurement types of Pleistocene lion remains showing a decreasing tendency from MIS 11-9 lions to younger samples. The MIS 17-12 lions show smaller values of morphometric parameters than lion remains dated as MIS 11-9. For other explanations see Fig. 6.

which differ substantially from all other groups in the crown breadth (B) of m1 (Fig. 5), anterior breadth (Ba) of P4 and p4 (Fig. 4H–S), posterior breadth (Bp) of P3, p3 and p4 (Fig. 4), total crown length (L) of canine, p3, p4 and m1 (Figs. 4 and 5), anterior breadth to the total crown length (Ba/L) and paracon length (Lpa) of P4 (Fig. 3) as well as posterior breadth to total crown length ratio (Bp/L) of P3 and p4 (Fig. 4). The most recent lion remains are also significantly smaller than those from MIS 17-12 and 11-9 groups in the maximal anteroposterior diameter of calcaneus and canine breadth (B). The MIS 5-2 remains are also smaller than the MIS 11-9 and 8-6 groups in total crown length (L) of P3 and P4 (Fig. 3), anterior breadth (Ba) of P3 (Fig. 4A–E), posterior breadth (Bp) and paracon height (Hpa) of P4 (Fig. 3), protoconid length (Lpr) of p4 (Fig. 4H–S), minimal transverse middle shaft diameter (mB) of metacarpus and metatarsus III as well as its ratio to the total length (mB/L) of metatarsus III. There are also significant differences between the MIS 5-2 and the MIS 11-9 groups in paracon length (Lpa) and the ratio of anterior breadth to the total crown length (Ba/L) of P3 (Fig. 4A–E), metastyl length (Lms) and posterior breadth to the total crown length ratio (Bp/L) of P4 (Fig. 3), protoconid length (Lpr), anterior breadth (Ba) and its ratio to the total crown length (Ba/L) and posterior breadth to the total crown length (Bp/L) of p3 (Fig. 4F–G), the minimal transversal middle shaft diameter to the total length ratio (mB/L) of metacarpus II, maximal anteroposterior diameter of distal (dL) and proximal epiphysis (pL) of metacarpus III, minimal transverse middle shaft diameter (mB) and maximal anteroposterior diameter of distal epiphysis (dL) and proximal epiphysis (pL) of metacarpus IV, maximal anteroposterior diameter of proximal epiphysis (pL) and total length (L) of metacarpus V as well as minimal transverse middle shaft diameter (mB) and its ratio to the total length (mB/L) of metatarsus V. The MIS 5-2 group differs from the MIS 8-6 group also in m1 paraconid to protoconid length ratio (Lpa/Lpr) (Fig. 5). Moreover, the MIS 8-6 group has significantly smaller total crown length (L) and breadth (B) of canine as well as breadth (B) of m1 than the oldest Pleistocene lions. The increase in the measurements from MIS 17-12 to MIS 11-9 followed by a decline to the MIS 5-2 period can be observed also for some measurements of limb bones, but the differences are not supported

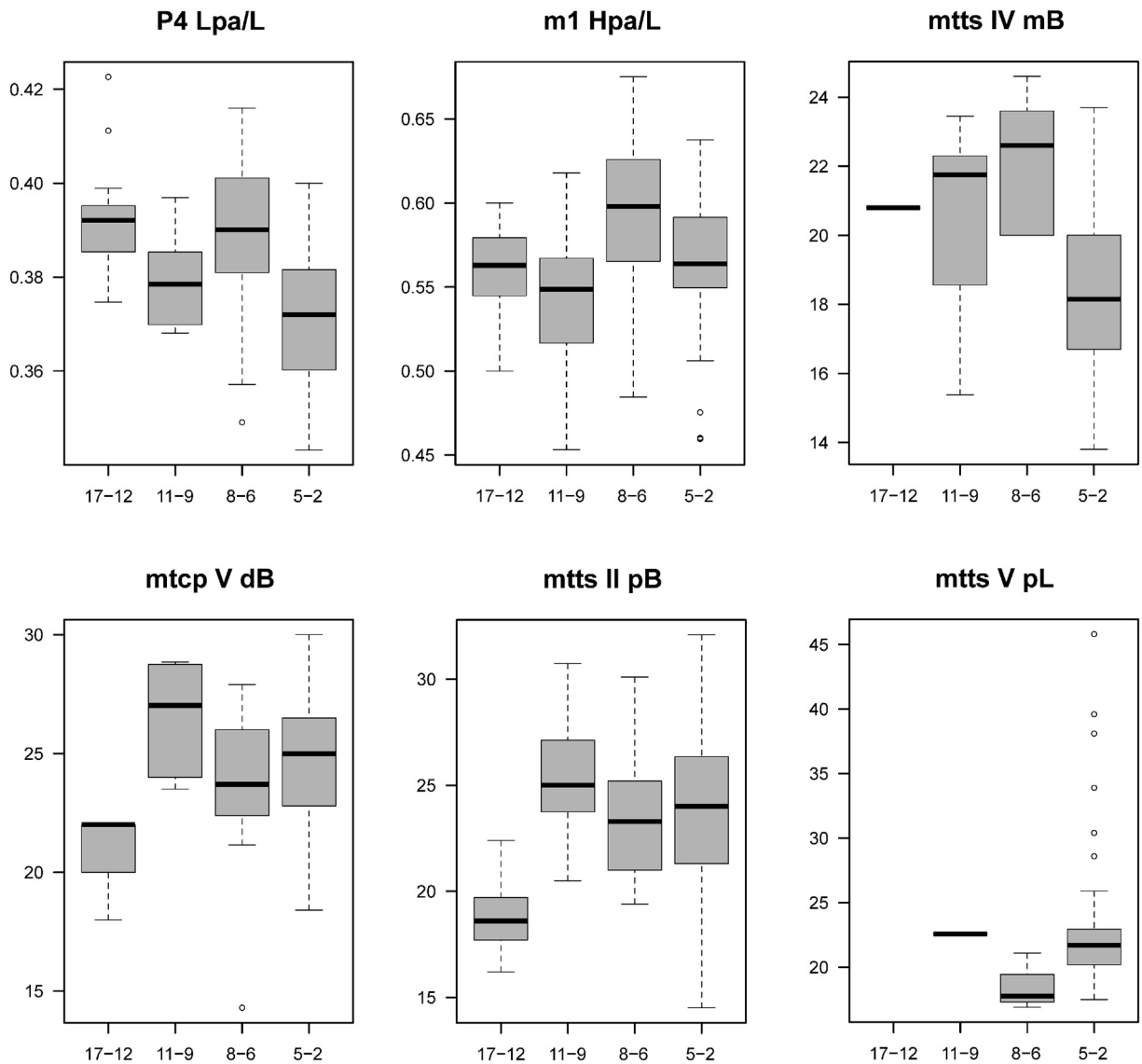

Fig. 9. Box-plots of selected measurement types of Pleistocene lion remains showing: (a) relatively big indices for MIS 8-6 lions (P4 Lpa/L, m1 Hpa/L, mtts IV mB); (b) relatively small measurements for MIS 17-12 lions (mtts II pB, mtcp V dB); (c) relatively small measurements for MIS 8-6 lions (mtts V pL). For other explanations see Fig. 6.

by statistical analyses (Fig. S4).

A deviation from the increasing or decreasing tendency is shown by the ratios: m1 paraconid height to total crown length (Hpa/L) and P4 paracon length to total crown length (Lpa/L) (Fig. 9). Their values decreased from MIS 17-12 to 11-9, and then they increased to MIS 8-6 reaching the maximum, subsequently they declined to MIS 5-2. These indices are significantly bigger in the MIS 8-6 lions than in those dated as MIS 11-9 and 5-2, while the latter index is smaller in MIS 11-9 and 5-2 groups than in the MIS 17-12 group (Fig. 9).

The MIS 8-6 displayed the biggest value of maximal transverse diameter of distal epiphysis (dB) and minimal anteroposterior middle shaft diameter (mL) of metatarsus IV (Fig. 9). In consequence, the MIS 5-2 lions were significantly smaller than those from MIS 8-6 in the maximal transverse diameter of distal epiphysis (dB) and the minimal anteroposterior middle shaft diameter (mL) of metatarsus IV, and also smaller than the MIS 11-9 lions in the minimal transverse middle shaft diameter (mB) of this bone. Moreover, the lion metatarsus V dated as MIS 8-6 and 5-2 had a significantly smaller maximal transverse diameter of proximal epiphysis (pB) than that from MIS 11-9, but the lack of this bone remains from MIS 17-12 period makes it impossible to assign this case to the above-described general trends (Fig. S4).

Unique values are those of the maximal transverse diameter of distal epiphysis (dB) of metacarpus V and the maximal transverse diameter of proximal epiphysis (pB) of metatarsus II (Fig. 9). The oldest group of lions is significantly smaller than the MIS 11-9 and 5-2 lions in terms of the maximal transverse diameter of distal epiphysis (dB), and also smaller than the MIS 8-6 lions in terms of the maximal transverse diameter of proximal epiphysis (pB). The other groups are statistically indistinguishable in respect of these measurements. Interestingly, the maximal anteroposterior diameter of proximal epiphysis (pL) of metatarsus V is significantly larger in the MIS 11-9 and 5-2 groups than in the MIS 8-6 group (Fig. 9). This is the third case, besides P4 metastyl length ratio to the crown total length (Lms/L) and paracon length (Lms/Lpa), when the stratigraphically youngest lions show significantly bigger values of the studied parameters than their direct predecessors (Fig. 9).

In order to further assess the observed morphometric trends over time, we calculated Spearman's correlation coefficients

between the individual measurements or indices and the rank of lion groups arranged according to the chronological order (Table S16). Eighty-one comparisons out of 143 turned out to be statistically significant with $p < 0.05$. Seventy-seven cases showed negative correlation and the Spearman's coefficient ρ varied from −0.2 to −0.65. The strongest negative correlation with $\rho < -0.5$ was shown by the total length (−0.55) and breadth (−0.58) of canine, anterior breadth of p3 (−0.51), anterior (−0.65) and posterior breadth of p4 (−0.53), as well as breadth (−0.53) and its ratio to the crown total length (−0.53) of m1. Only four variables were positively and significantly correlated with the rank of the stratigraphical lion groups: p4 protoconid length ratio to crown total length (0.36), P4 metastyl length ratio to crown total length (0.44), as well as ratios of P3 anterior to posterior breadth (0.46) and P4 metastyl length to paracon length (0.67).

4.2. Summary of statistical comparisons of Panthera spelaea groups

The statistical analyses of *P. spelaea* over time show that the MIS 11-9 and MIS 5-2 groups differ significantly in the largest percentage of possible variables both for teeth and bones, i.e. 64% and 31% respectively, while the MIS 17-12 and 8-6 groups differ in the smallest percentage of parameters, i.e. 11% and 5%, respectively (Table 2). The greater number of measurements and indices has significantly smaller values in the remains dated as MIS 17-12 than as MIS 11-9. In turn, the MIS 17-12, 11-9 and 8-6 remains are mostly bigger than those from the MIS 5-2 period. The MIS 11-9 remains often show larger measurements and indices than those from MIS 8-6.

Table 2. The number and percentage of cases for which statistically significant differences were found in the comparisons of four stratigraphical groups of *P. spelaea*. All possible cases are also shown. The term 'significantly bigger' means that the first group in the comparison has measurements values significantly bigger than the second group. The term 'significantly smaller' means that the measurement values are smaller in the first group.

In the same way, we summarised the results for the teeth and bone types (Table 3). Generally, the teeth separate the lion groups better than the tarsal, metatarsal and metacarpal bones. There are two to three times more diagnostic dental measurements and indices than those for the bones. The most discriminative are the measurements and indices of canine. More than 72% of all possible comparisons involving these parameters were statistically significant. A quite high percentage of statistically discriminative parameters refer also to the fourth upper (53%) and lower (47%) premolars as well as metatarsus V (40%). The least diagnostic are the lengths and their ratio of P3 and P4 premolars present in the same upper jaw. None of these parameters showed statistically significant differences between the compared groups, probably because of the small samples of jaws with both teeth preserved.

Table 3. Number and percentage of remain types for which statistically significant differences were found in comparisons of four stratigraphical groups of P. spelaea. All possible comparisons are also shown.

Crown breadth of teeth and its ratio to length (B/L) turned out to be the best to separate the lion groups (Table 4). Seventy-five percent of all possible comparisons involving this type of measurements were statistically significant. A quite good

Table 3
The number and percentage of remain types for which statistically significant differences were found in the comparisons of four stratigraphical groups of *P. spelaea*. All possible comparisons were also shown.

Remain type	Significant cases	All possible	Percent of significant
C	13	18	72.2
P3	16	60	26.7
P4	41	78	52.6
p3	16	60	26.7
p4	28	60	46.7
m1	30	90	33.3
P3 to P4	0	18	0.0
p3 to p4	3	18	16.7
p3 to m1	4	18	22.2
p4 to m1	6	18	33.3
mtcp II	2	31	6.5
mtcp III	8	42	19.0
mtcp IV	4	45	8.9
mtcp V	6	30	20.0

Table 4
The number and percentage of dental measurements types for which statistically significant differences were found in the comparisons of four stratigraphical groups of *P. spelaea*. All possible comparisons were also shown.

Parameter	Significant cases	All possible	Percent of significant
B	9	12	75
B/L	9	12	75
Ba	15	24	62.5
Ba/Bp	1	18	5.6
Ba/L	8	24	33.3
Bp	16	24	66.7
Bp/Ba	0	6	0
Bp/L	11	24	45.8
Hin	2	6	33.3
Hin/L	2	6	33.3
Hpa	4	18	22.2
Hpa/Hpr	0	6	0
Hpa/L	4	18	22.2
Hpr	3	18	16.7
Hpr/L	0	18	0
L	24	36	66.7
Lm1	3	12	25
Lms	2	6	33.3
Lms/L	4	6	66.7
Lms/Lpa	4	6	66.7
LP3	4	18	22.2
Lp3/Lm1	0	6	0
LP3/LP4	0	12	0

Table 2
The number and percentage of cases for which statistically significant differences were found in the comparisons of four stratigraphical groups of P. spelaea. All possible cases were also shown. The term 'significantly bigger' means that the first group in the comparison has a measurement type significantly bigger than the second group. The term 'significantly smaller' means that a measurement type is smaller in the first group.

Type of remains	Cases	MIS 17-12 vs MIS 11-9	MIS 17-12 vs MIS 8-6	MIS 17-12 vs MIS 5-2	MIS 11-9 vs MIS 8-6	MIS 11-9 vs MIS 5-2	MIS 8-6 vs MIS 5-2
Teeth	Significantly bigger	2	5	28	18	44	31
	Significantly smaller	15	3	4	2	3	2
	All possible	73	73	73	73	73	73
	Percent of significant	23.3	11.0	43.8	27.4	64.4	45.2
Bones	Significantly bigger	0	1	5	9	20	11
	Significantly smaller	3	1	2	0	0	1
	All possible	37	39	39	62	64	68
	Percent of significant	8.1	5.1	17.9	14.5	31.3	17.6

discriminatory power was also shown by anterior (Ba) and posterior (Bp) breadth, crown total length (L) as well as ratio of metastyl length to crown total length (Lms/L) and to paracon length (Lms/Lpa). More than 62% of comparisons involving anterior breadth and almost 67% of the other parameters were significant. The parameters concerning tarsal and metapodial bones less often separated the groups than dental traits (Table 5). Only 28% and 27% intergroup comparisons based respectively on the minimal transverse diameter in the middle shaft (mB) and the metapodial length showed significant differences in statistical tests.

Table 4. Number and percentage of dental measurements for which statistically significant differences were found in comparisons of four stratigraphical groups of *P. spelaea*. All possible comparisons are also shown.

Table 5. Number and percentage of tarsal and metapodial measurements for which statistically significant differences were found in comparisons of four stratigraphical groups of *P. spelaea*. All possible comparisons are also shown.

The revision of Polish records of *P. s. fossilis* mentioned by previous authors (Barycka, 2008; Marciszak and Stefaniak, 2010; Marciszak et al., 2014) in all cases confirmed their earlier diagnosis. Additionally, new material from other Polish sites extends the distribution of the steppe to include another five localities. Among them Draby is the northernmost site in Central Europe, where remains of this lion were found.

The analysis of more numerous postcranial bones provided less valuable information, and showed a greater variability than those of cranial or dental material (Tables S9–S12). The massiveness of metapodials, counted as the minimal median shaft breadth to the total bone length index, showed no particular differences between *P. s. fossilis* and *P. s. spelaea*, except the metatarsus II, III and V, which were more robust in *P. s. fossilis*. However, the limited number of the material of this form should be kept in mind. Similarly, the slight differences in the morphology of muscle joints and articular surfaces should be interpreted as an intraspecific variation. It can be concluded that metapodials, carpals and tarsals are actually almost indistinguishable morphologically (Tables S9–S12).

4.3. Percentage difference in measurements and the rate of change over time

In order to compare all the measurements simultaneously and to asses their direction of changes over time, we calculated the percentage difference (D) in median of each variable between chronologically subsequent lion groups (Table S17). A positive value of D indicates that the measurement increased in the younger group (potential descendant), compared to the older group (ancestor). A negative value means that the measurement decreased over time. We compared the MIS 11-9 group with the MIS 17-12 group, the MIS 8-6 with the MIS 11-9 group, and the MIS 5-2 with the MIS 8-6 group. The distributions of D values are presented separately for teeth and bone measurements, the indices in Fig. 10. The distributions of D for teeth are unimodal, while those for bones are multimodal in the case of the MIS 8-6 vs 11-9 comparison and especially MIS 11-9 vs 17-12 comparison. It suggests a varied pattern of change in the limb bones.

The distributions of the MIS 11-9 vs MIS 17-12 comparison tend to assume positive values, while the other distributions are shifted toward negative values (Fig. 10). In the case of the first comparison, 71% (52 out of 73) of teeth measurements and 72% (46 out of 64) of bone measurements show larger values in the younger group than the oldest, which indicates an increase over time. In contrast, 78% (57 out of 73) and 81% (59 out of 73) of the teeth measurements decreased from MIS 11-9 to 8-6 and from MIS 8-6 to 5-2, respectively. More than 77% (54 out of 70) and 70% (49 out of 70) of the bone measurements also became smaller in the respective younger groups than in their ancestors.

Considering only the 15%-changes and variables represented by at least three samples, it can be seen that the largest decrease in the studied measurements from MIS 17-12 to 11-9 affected the ratio of paracon height to crown total length (Hpa/L) of P3; the maximal anteroposterior diameter of proximal epiphysis (pL) of metatarsus III as well as the minimal transverse middle shaft diameter (mB) and its ratio to the total length (mB/L) of metatarsus II (Table S17). In turn, the following parameters increased by more than 15% during that period: anterior breadth (Ba) of P3 and p3; posterior breadth (Bp) of P3, P4, p3 and p4; paracon length (Lpa) of P3; paracon height (Hpa) of P4, crown total length of p3 and p4 obtained in measurements of two premolars in the same maxilla, maximal transverse diameter (B) and its ratio to maximal anteroposterior diameter (B/L) of calcaneus; maximal transverse diameter of distal epiphysis (dB), minimal anteroposterior middle shaft diameter (mL) and maximal anteroposterior diameter of proximal epiphysis (pL) of metacarpus III; maximal transverse diameter of distal (dB) and proximal (pB) epiphysis of metacarpus V; maximal transverse (pB) and anteroposterior (pL) diameter of proximal epiphysis of metatarsus II; minimal transverse middle shaft diameter ratio to total length (mB/L) of metatarsus III.

Adopting the same 15%-threshold, in the next transition (from MIS 11-9 to 8-6) only the maximal transverse diameter of distal epiphysis (dB) of metacarpus II increased greatly, but the following parameters decreased: crown breadth (B) and length (L) of canine; posterior breadth (Bp) of p3; maximal transverse diameter (B) of calcaneus; maximal anteroposterior diameter of distal epiphysis (dL) of metacarpus III; maximal transverse diameter of proximal epiphysis (pB) and maximal anteroposterior diameter of distal epiphysis (dL) of metacarpus V; minimal transverse middle shaft diameter (mB), maximal transverse diameter of distal (dB) and proximal epiphysis (pB) as well as maximal anteroposterior diameter of proximal epiphysis (pL) of metatarsus V.

In the comparison of MIS 8-6 and 5-2, only the maximal anteroposterior diameter of proximal epiphysis (pL) of metatarsus V increased at the same >15%-level, while the decrease affected posterior breadth (Bp) of P3; maximal transverse diameter of distal epiphysis (dB) as well as minimal transverse (mB) and anteroposterior (mL) middle shaft diameter of metatarsus IV.

Generally, the percentage difference expressed by the median calculated for the absolute D values for teeth measurements is largest for the comparison of MIS 11-9 and 17-12 lions, 5.84%. This parameter is smaller, i.e. 4.89% and 4.64%, for the MIS 8-6 vs 11-9 and MIS 8-6 vs 5-2 comparisons, respectively. For the studied limb bones, these values are 11.54%, 6.80% and 4.81%, respectively. Since the analysed groups contain remains from different time ranges, we normalized the median absolute D values by the corresponding

Table 5
The number and percentage of tarsal and metapodial measurements types for which statistically significant differences were found in the comparisons of four stratigraphical groups of *P. spelaea*. All possible comparisons were also shown.

Parameter	Significant cases	All possible	Percent of significant
B	1	12	8.3
B/L	2	12	16.7
dB	4	36	11.1
dL	3	16	18.8
L	13	48	27.1
mB	11	39	28.2
mB/L	5	33	15.2
mL	1	32	3.1
pB	5	42	11.9
pL	8	39	20.5

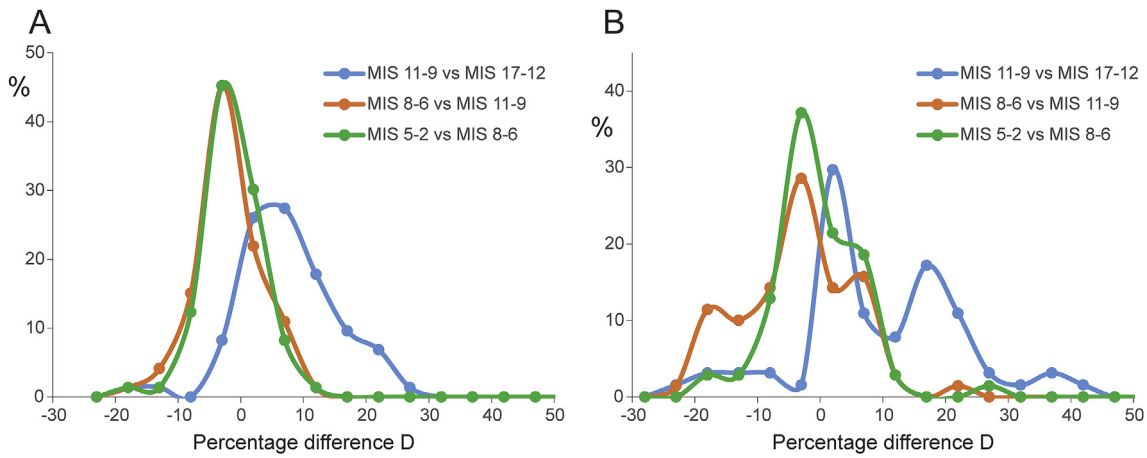

Fig. 10. Distributions of percentage difference D in median of the variables between chronologically consecutive lion groups separately for teeth (A) and bone (B) measurements and indices.

time span in order to obtain the rate of change in D for 100 ka. The normalized D for the teeth measurements is 1.42%, 1.66% and 1.62% for MIS 11-9 vs 17-12, MIS 8-6 vs 11-9 and MIS 8-6 vs 5-2 comparisons, respectively. For the bone measurements, we obtained the following values: 2.80%, 2.31% and 1.68%. The results mean that the greatest changes in teeth occurred on the transition from MIS 11-9 to 8-6 and were quite considerable in the next period, while bones changed at the highest rate between MIS 17-12 and 11-9 and then the rate decreased.

5. Discussion

P. s. fossilis represents the first immigration wave of lion to Europe, most probably from Africa. According to Barycka (2008), such migrations started in MIS 13-12. A clearly visible transformation took place in MIS 11 and later. It occurred earlier in Eastern and South-Eastern Europe, and then spread through Central to the Western Europe (Schütt and Hemmer, 1978; Baryshnikov and Tsoukala, 2010). The evolutionary changes began from the lower dentition, and started with the shortening and lowering of the main cusps on p3 and p4 as well as narrowing of p3, p4 and m1 crowns. The p4/m1 index changed little, while in upper dentition, only the lowering of the main cusp on P3 and the elongated metastyl on P4 were noted. The lion from MIS 11-9 is classified as a *P. s. fossilis*, however, the morphology of individuals from this interval is characterised by more progressive features and can be regarded as a more advanced evolutionary stage. These changes were first found in eastern lions, e.g. from Hungary (Hanko, 2007), Greece (Baryshnikov and Tsoukala, 2010) and western Russia (Barycka, 2008). Simultaneously, still very large lions, but with narrower carnassials, and with elongating cutting surfaces of teeth, were present in Germany and France (Groiss, 1992; Argant and Brugal, 2017). It seems that morphological changes took place independently in Europe, in autochthonous populations which had existed since the early Middle Pleistocene. Next, new and more evolutionarily advanced lions appeared in Europe due to migration waves from the east. These lions were already so distinct from the typical *P. s. fossilis*, that they were once classified as *P. s. spelaea* (Vereschagin, 1971; Sabol, 2011b).

The lions of the next period (MIS 8-6) were characterised by a more mosaic variation in their morphology. These intermediate forms evolved into *P. s. spelaea*, which appeared for the first time in MIS 6 and still showed a great size as well as some ancestral morphological features (Argant, 1991; Argant et al., 2007; Barycka, 2008; Marciszak et al., 2014; Sabol, 2014; Argant and Brugal, 2017). Visible morphometric changes appeared in upper dentition in MIS 6-5 and were next established in the stratigraphically later *P. s. spelaea*. This time interval is documented by the presence of mixed forms: large individuals with somewhat conservative features along with lions having a smaller and evolutionarily more advanced dentition (Argant, 1991; Hemmer, 2011; Marciszak et al., 2014). At that time, eastern lions showed a more advanced morphology compared with those from Western Europe (Schütt and Hemmer, 1978; Barycka, 2008; Hemmer, 2011; Sabol, 2011b).

In this context, the territory of Poland can be regarded as a migration corridor linking eastern and western parts of Europe. Extensive, flat Polish lowlands, without sufficient geographical barriers, were ideal areas for dispersal and migration of large herbivore herds, being the main lion prey. Our results indicate that the earliest Polish records of *P. spelaea* from Tunel Wielki and Południowa caves, classified as *P. s. fossilis*, are indistinguishable from the specimens from Mauer or Mosbach 2. Therefore, they can represent descendants of the oldest lions which entered Europe. The more advanced form of *P. s. fossilis* appeared in the late Middle Pleistocene (MIS 11-9), and is known from the lowermost sediments of caves Wierzchowska Górna, Deszczowa and Biśnik. They differ from the typical *P. s. fossilis* from the mid Middle Pleistocene sites (MIS 16-12) in its proportionally shorter p4, premolars with lower and shorter main cusps and more reduced additional cusplets. At the same time, this form was still ancestral and giant, having massive carnassials with proportionally short cutting surfaces, broad premolars and massive limb bones. From the palaeobiogeographical point of view, these evolutionary changes could result from both the eastern immigrations and evolution *in situ* (Sabol, 2011b; Masseti and Mazza, 2013).

6. Conclusions

P. s. fossilis is a member of the European Middle Pleistocene faunal assemblages. It differs from the typical chronoform, the cave lion *P. s. spelaea*, in, on average, larger size and teeth proportions. The occurrence of this chronoform is documented in Poland by five mid and late Middle Pleistocene sites - caves: Tunel Wielki, Południowa, Draby, Biśnik and Wierzchowska Góra caves. The study of the fossil material showed that the lions from Tunel Wielki and Południowa caves were very similar in morphology and size to the typical *P. s. fossilis* from Mosbach 2 and Mauer. The lion material from Poland analysed in this paper is also represented by a typical *P.*

s. fossilis, i.e. a large form with robust stature and conservative dental morphology. Stratigraphically younger lions dated as MIS 11-9/8, represent the second form, known from caves Draby, Deszczowa, Biśnik and Wierzchowska Górna. The lions from that period were even larger and more massive, but with more advanced dental features. The lions from these two groups, the first from MIS 17-12, and the second, from MIS 11-9, turned out to be morphologically heterogeneous but homogeneous metrically. *P. s. fossilis* was also homogeneous spatially and temporally. It was comparatively large throughout the Middle and late Middle Pleistocene (MIS 20-9). Our analysis also showed that *P. s. fossilis* survived in Europe until MIS 9, still in large but already more advanced form. The lions from MIS 17-9 clearly differed from the younger ones. Since MIS 8, the lion became smaller in many dental and long bone measurements.

We described numerous lion remains from seven Polish excavation sites dated from MIS 15-13 to MIS 9. All the remains showed high similarity to *P. s. fossilis*. Including these results and all available data from literature, we classified the lion remains into four groups according to their palaeoclimatic age: MIS 17-12 (712-424 ka), MIS 11-9 (424-300 ka), MIS 8-6 (300-130 ka) and MIS 5-2 (130-14 ka). These groups correspond also to evolutionary stages recognised in the lion history, i.e. the typical *P. s. fossilis*, the advanced *P. s. fossilis*, *P. s. intermedia* and *P. s. spelaea*. Our comparative analyses revealed significant differences in all pairwise comparisons between these groups.

Dental features turned out to be more diagnostic and demonstrated more significant differences than the tarsal and metapodial bones. It means that teeth evolved at the highest rate and can provide the most valuable data for biochronological analysis. The largest fraction of statistically discriminative traits was displayed by the canine, P4, p4 and, interestingly, metatarsus V. The most significant changes involved crown breadth and its ratio to crown length, anterior and posterior breadth, crown total length as well as ratio of metastyl length to crown total length and to paracon length.

Overall, most measurements decreased over time, which indicates that the lion became smaller. As a result of this trend, the MIS 5-2 lion represents the smallest form. However, the continuous decrease in the values of most features started in MIS 11-9, because the oldest remains dated to MIS 17-12 were usually smaller in many measurements than in their direct descendants. It suggests that the oldest forms were replaced by larger ones. In the transition from the oldest to the younger forms, bones were subject to the greatest changes, while in the evolution from MIS 11-9 lions to their descendants, teeth changed to the greatest extent. The limb bones usually increased in size and thickness from MIS 17-12 to 11-9, which could be related to the occurrence of forms better adapted to migrations or confrontation with large prey. In turn, the general decrease in teeth size and changes in their morphology in other periods (since MIS 8) suggest that the stratigraphically younger forms could prefer smaller prey.

Interestingly, not all characters followed the general trends. Different direction of changes was shown mostly by the tarsal and metapodial bones, which indicates a mosaic evolution of limb skeleton. Only very few traits increased in the evolution of MIS 5-2 lions. One of them is the greatest ratio of P4 metastyl length to crown total length and to paracon length. The relative lengthening of the metastyl can be associated with a greater importance of this edge in food cutting in cooperation with the other carnassial, i.e. m1.

Our statistical and comparative analyses revealed the following changes in the lion remains over time:

1) C1
   - from MIS 8: the tooth shortened and narrowed; it narrowed in relation to its length;
2) P3
   - from MIS 11: the anterior part widened in relation to the posterior part; the paracon lowered in relation to the whole tooth length; additional cusplets and cingulum started to reduce;
   - in MIS 11-9: the tooth lengthened and widened; the paracon lengthened;
   - from MIS 8: the tooth shortened and narrowed (also in relation to its length); the anterior part narrowed in relation to the whole tooth length; the paracon was shortening;
   - from MIS 5: the paracon lowered;
3) P4
   - The paracon length in relation to the whole tooth length fluctuated from greater (in MIS 17-12) to shorter (in MIS 11-9), next to greater (in MIS 8-6) and again to shorter values (in MIS 5-2);
   - from MIS 11: the metastyl was lengthened in relation to the paracon and the whole tooth; the parastyl increased; the protocon decreased; the preparastyl and the incipient cingulum in front of the parastyl developed;
   - in MIS 11-9: the tooth lengthened and widened; the paracon lengthened and elevated; the metastyl lengthened;
   - from MIS 8: the tooth shortened and narrowed (also in relation to its length); the paracon shortened and lowered; the metastyl shortened;
   - from MIS 5: the paracon lowered in relation to the whole tooth length;
4) p3
   - in MIS 11-9: the tooth lengthened and widened (also in relation to its length); the protoconid lengthened; the anterior part widened in relation to the whole tooth length;
   - from MIS 8: the tooth shortened and narrowed (also in relation to its length); the anterior part narrowed in relation to the whole tooth length; the protoconid shortened;
5) p4
   - from MIS 11: the protoconid lengthened in relation to the whole tooth; the protoconid lowered; the protoconid lowered in relation to the whole tooth length;
   - in MIS 11-9: the tooth lengthened and widened; the protoconid lengthened;
   - from MIS 8: the tooth shortened and narrowed (also in relation to its length); the anterior part narrowed in relation to the whole tooth length; the protoconid shortened;
6) m1
   - from MIS 11: the protoconid shortened (also in relation to the whole tooth length); the paraconid shortened in relation to the whole tooth length; the median bulge, the talonid and the zigzag enamel structure began to disappear, although they are still well visible in teeth from this period;
   - from MIS 8: the tooth shortened and narrowed (also in relation to its length); the incisor height was lowering (also in relation to the whole tooth length);
   - in MIS 8-6: the paraconid elevated in relation to the whole tooth length;
   - from MIS 5: the paraconid lowered (also in relation to the whole tooth length); the paraconid shortened (also in relation to the protoconid and the whole tooth length);
7) P3 to P4
   - from MIS 11: P3 lengthened in relation to P4
8) p4 to m1

- from MIS 5: p4 shortened in relation to m1

9) metacarpus II
   - from MIS 8: the anteroposterior diameter of distal epiphysis decreased; the middle shaft anteroposterior diameter decreased; the middle shaft transverse diameter decreased (also in relation to the whole bone length);
   - in MIS 8-6: the middle shaft anteroposterior diameter increased;
10) metacarpus III
   - in MIS 11-9: the anteroposterior diameter of epiphyses and the middle shaft diameters increased;
   - from MIS 8: the anteroposterior diameter of epiphyses decreased; the middle shaft transverse diameter decreased; the middle shaft anteroposterior diameter decreased;
   - from MIS 5: the bone shortened; the transverse diameter of distal epiphysis decreased;
11) metacarpus IV
   - in MIS 11-9: the anteroposterior diameter of epiphyses as well as of the middle shaft increased;
   - from MIS 8: the anteroposterior diameter of proximal epiphysis and the middle shaft diameters decreased; the anteroposterior diameter of distal epiphysis decreased;
   - from MIS 5: the bone shortened; the transverse diameter of distal epiphysis decreased;
12) metacarpus V
   - from MIS 11: the transverse diameter of distal epiphysis increased;
   - in MIS 11-9: the bone lengthened; the transverse diameter of proximal epiphysis increased;
   - from MIS 8: the bone shortened; the anteroposterior diameter of epiphyses decreased;
13) metatarsus II
   - from MIS 11: the transverse diameter of proximal epiphysis increased; the middle shaft transverse diameter in relation to the bone length decreased;
   - from MIS 5: the bone shortened; the middle shaft diameter decreased;
14) metatarsus III
   - in MIS 11-9: the middle shaft transverse diameter and its ratio to the bone length increased;
   - from MIS 8: the bone shortened; the middle shaft transverse diameter and its ratio to the bone length decreased;
   - from MIS 5: the transverse diameter of distal epiphysis decreased;
15) metatarsus IV
   - from MIS 5: the bone shortened; the middle shaft and distal epiphyses diameters decreased;
16) metatarsus V
   - from MIS 8: the bone shortened; the anteroposterior diameter of distal epiphysis as well as the transverse diameter of epiphyses decreased; the middle shaft anteroposterior as well as the middle shaft transverse diameter and its ratio to the bone length decreased;
   - from MIS 5: the anteroposterior diameter of proximal epiphysis increased;
17) calcaneus
   - from MIS 8: the bone narrowed and shortened;
18) talus
   - from MIS 11: the bone narrowed in relation to its length;
   - from MIS 8: the bone shortened and narrowed.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2019.105950.

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