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## *Panthera spelaea* (GOLDFUSS 1810) from North-Western Croatia

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**Key words:** Cave lion, *Panthera spelaea*, Evolution, Pleistocene, Croatia.

**Ključne riječi:** špiljski lav, *Panthera spelaea*, evolucija, pleistocen, Hrvatska.

### Abstract

The comparative analysis of the cave lion teeth ( $M_1$  and  $P^4$ ) from North-western Croatian Pleistocene sites (Veternica, Velika pećina and Vindija caves) indicated the presence of Middle and Upper Pleistocene forms of this species. Some common characteristics of stratigraphically younger populations of the cave lion from North-western Croatia and the Repolusthöhle population, suggest that Croatian populations belong to the Westeuropean lineage with special characteristics.

### Sažetak

Komparativna analiza zubiju ( $M_1$  i  $P^4$ ) vrste *Panthera spelaea* iz pleistocenskih nalazišta sjeverozapadne Hrvatske (špilja Veternice, Velike pećine i Vindije) upućuje na prisutnost srednjo i gornjopleistocenskih oblika te vrste. Na osnovi nekih zajedničkih karakteristika stratigrafski mlađih populacija špiljskog lava iz sjeverozapadne Hrvatske i Repolusthöhle populacije može se pretpostaviti pripadnost naše populacije zapadnoeuropskoj razvojnoj liniji s posebnim značajkama.

## 1. INTRODUCTION

Fossil remains of the cave lion are not uncommon in European Pleistocene sites. At North-western Croatian sites, according to their number, remains closely resemble cave bear and wolf. From a preliminary examination of fossil remains, a relatively high degree of morphologic heterogeneity was noticed independently of stratigraphical position.

The previously known evolution of the cave lion (SCHÜTT, 1969; HEMMER, 1974; SCHÜTT & HEMMER, 1978; ARGANT, 1991) was based upon the metrical features of the first lower molar, and the fourth upper premolar.

Comparative analysis of cave lion (*Panthera spelaea*) teeth, was performed as part of the palaeontological and palaeobiological studies of the large fossil carnivores from North-western Croatia for a doctoral thesis (GUŽVICA, 1996). The objectives of this study were to further determine the microevolutional changes of the cave lion teeth, and to determine the position of cave lion populations from the Pleistocene of North-western Croatia, relative to similar populations from other European sites.

## 2. MATERIAL AND METHODS

The material used for comparative analysis of cave lion teeth originated from three Pleistocene sites of North-western Croatia: Veternica cave (MALEZ, 1963, 1965), Velika pećina cave (MALEZ, 1986) and Vindija cave (MALEZ & RUKAVINA, 1975; MALEZ et al., 1984). The fossil remains of the cave lion from Velika pećina and Veternica had been previously partly analysed in the studies by MALEZ (1963, 1986) and was therefore subjected to revision. The material from Vindija cave was determined and analysed for the first time. For the comparative analysis, the sixteen first lower molars ( $M_1$ ) and the fourth upper premolars ( $P^4$ ) with preserved crowns were used. Some of the teeth were isolated, and some were in the lower, and upper jaws respectively. The fossil material was stored in the Department of Palaeontology and Quaternary Geology of the Croatian Academy of Sciences and Arts in Zagreb.

Metric analysis was performed according to SCHMID (1940), and the results were rounded to the accuracy of 0.1 mm. Besides the metric values, indices were calculated (as %-age values) which express the relationships between particular dimensions. The estimation of body weight was performed by computer program CARNI (GUŽVICA & PETROVIĆ, 1990) based on the LEGENDRE & ROTH (1988) method according to the interdependence of the tooth crown surface of the first lower molar ( $M_1$ ) and body weight.

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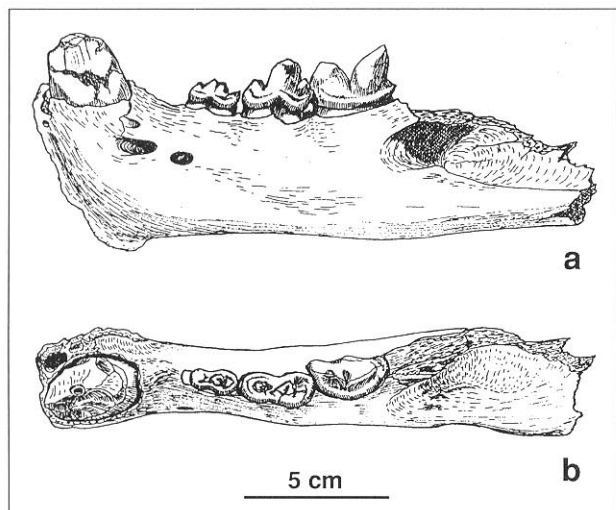


Fig. 1 Left lower jaw (inv. no. 175/car) of *Panthera spelaea* from layer "i<sub>g</sub>" of Velika pećina: a) lateral view; b) dorsal view.

### 3. RESULTS

#### 3.1. COMPARATIVE ANALYSIS

For the comparative analysis of the cave lion teeth from Vindija, four first lower molars ( $M_1$ ) were separated from the layers "M", "J", "G" and "G<sub>4+5</sub>", and two fourth upper premolars ( $P_4$ ) one of which originated from the layer "H", but the stratigraphical position of the other is unknown. From the layer "i<sub>g</sub>" of Velika pećina, the lower jaw with a well-preserved  $M_1$  was separated (Fig. 1), and from the layer "f" of Veternica cave the upper jaw with a well-preserved tooth was separated (Fig. 2).

##### 3.1.1. The first lower molar - $M_1$

The first left lower molar from the layer "M" of Vindija cave is well-preserved and belongs to the mandible with inventory number 13/car (Fig. 3). On the buccal side, the paraconid and protoconid were considerably worn as a result of occlusion with  $P^4$ . The pointed protoconid dominates over the paraconid. The border of the crown base with emphasised cingulum at the lingual side is pronounced. The indices calculated for this tooth are not strictly indicative (Table 1), although their values do fit into the range of variation observed in the Middle Pleistocene and Upper Pleistocene forms of fossil lions. However, it was noticed that they did not trend towards the average values of stratigraphically younger forms but approach the borderline values of stratigraphically older forms. The wide distribution of indices points to the fact that the  $M_1$  from the layer "M" of Vindija cave integrates the metric characteristics of the Middle as well as the Upper Pleistocene forms of *Panthera spelaea*. Based on the correlation diagrams (Figs. 4 & 5), and characteristics mentioned so far, the lower jaw from the layer "M" of Vindija

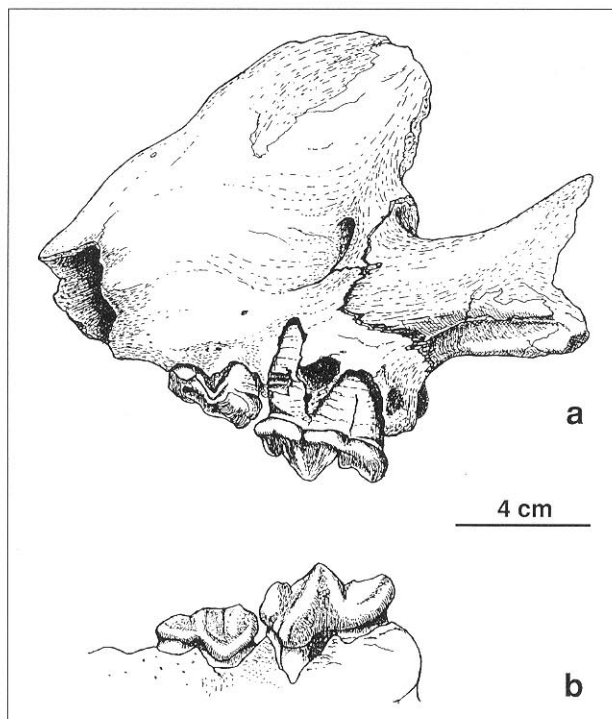


Fig. 2 Left upper jaw (inv. no. 600/car) of *Panthera spelaea* from layer "f" of Veternica cave: a) lateral view; b) teeth, medial view.

cave could belong to a Middle Pleistocene form of *Panthera spelaea*.

From the layer "J" of Vindija cave, the first right lower molar (332/car) was separated. The tooth crown is well-preserved, while the aboral root of the tooth is missing. At the buccal side of the protoconid, and specially the paraconid, wearing traces of an unusual shape were observed, being the result of irregular occlusion. At the lingual side, instead of the cingulum there are three small, pointed cusps which are very unusual for  $M_1$ . Although most of the indices are not indicative, the indices 4/1 and 6/1 (Table 1) suggest an Upper Pleistocene form of cave lion. This is further supported by

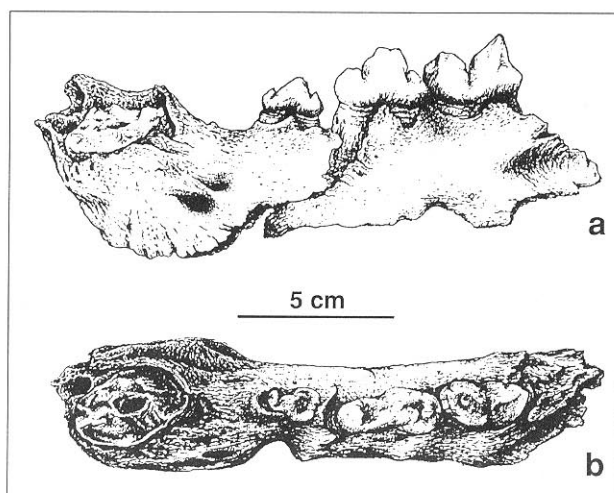


Fig. 3 Left lower jaw (inv. no. 13/car) of *Panthera spelaea* from layer "M" of Vindija cave: a) lateral view; b) dorsal view.

	1 (mm)	2 (mm)	2/1 (%)	3 (mm)	3/1 (%)	3/2 (%)	4 (mm)	4/1 (%)	5 (mm)	5/1 (%)	5/2 (%)	6 (mm)	6/1 (%)	6/4 (%)
<i>P. spelaea</i> , Vindija, 13/car, "M"	30.9	18.6	60.2	16.8	54.4	90.3	16.7	54.0	17.2	55.7	92.5	10.7	34.6	64.1
<i>P. spelaea</i> , Vindija, 332/car, "J"	33.5	20.1	60.0	18.9	56.4	94.0	16.6	49.6	18.8	56.1	93.5	10.6	31.6	63.9
<i>P. spelaea</i> , Vindija, 328/car, "G"	28.2	17.9	63.5	15.0	53.2	83.8	14.1	50.0	15.2	53.9	84.9	6.6	23.4	46.8
<i>P. spelaea</i> , Vindija, 323/car, "G <sub>4-5</sub> "	33.7	20.9	62.0	17.9	53.1	85.6	16.6	49.3	16.8	49.9	80.4	9.6	28.5	57.8
<i>P. spelaea</i> , Velika pečina, 175/car, "g"	29.8	18.7	62.8	15.4	51.7	82.4	14.7	49.3	16.9	56.7	90.4	9.6	32.2	65.5
<i>P. spelaea</i> , Vérteszöllös (JÁNOSSY, 1969)	28.7	17.5	61.0	15.5	53.0	88.5	15.5	53.0	18.0	63.0	103.0	9.0	31.0	58.0
<i>P. spelaea</i> , Dechenhöhle (DIETRICH, 1968)	28.6	17.7	62.0	15.3	53.5	86.5	15.4	54.0	16.4	57.5	92.5	9.8	34.5	63.5
<i>P. spelaea</i> , Hunas (HELLER, 1966)	30.2	19.0	63.0	16.5	55.0	87.0	16.4	54.5	17.4	57.5	91.5	10.3	34.0	63.0
<i>P. spelaea</i> , Burgtonna (DIETRICH, 1968)	30.5	18.9	62.0	16.2	53.0	86.0	15.5	51.0	18.2	59.5	96.5	10.4	33.5	67.0
<i>P. spelaea</i> , Ehringsdorf (DAXNER-HÖCK, 1975)	32.7	20.0	61.0	17.4	53.0	87.0	16.4	50.0	18.2	55.5	91.0	11.7	36.0	71.5
<i>P. spelaea</i> , Azé (ARGANT, 1991)	31.3	18.2	58.1	18.5	59.1	101.6	17.6	56.2	18.2	58.1	100.0	10.4	33.2	59.0
<i>P. mosbachensis</i> , Château (ARGANT, 1991)	32.9	19.5	59.2	20.4	62.0	104.6	18.6	56.5	19.0	57.7	97.4	12.0	36.4	64.5
<i>P. leo fossilis</i> (SCHÜTT & HEMMER, 1978)	27.8	17.0	59.0	15.5	53.5	86.0	15.3	53.5	15.8	55.5	90.0	10.5	34.0	63.5
n=8	32.9	19.4	63.5	18.8	57.0	97.0	18.6	56.5	18.6	59.0	96.0	12.7	38.5	68.5
<i>P. leo spelaea</i> (SCHÜTT & HEMMER, 1978)	29.8	18.5	61.5	16.8	55.0	89.5	16.4	55.5	17.2	57.0	93.0	11.0	36.0	65.0
n=18	26.4	15.7	56.5	13.5	50.0	83.0	13.5	45.5	14.0	51.5	84.0	7.6	28.5	56.0
Repolsthöhle (SCHÜTT & HEMMER, 1978)	31.7	18.9	61.5	17.0	57.0	96.0	16.2	55.0	17.0	56.5	95.5	10.5	35.0	68.0
n=10	28.9	17.2	59.5	15.3	53.5	89.0	14.7	51.0	15.2	53.0	89.0	9.0	31.0	61.0
<i>P. leo</i> (recent) (SCHMIDT, 1940)	26.8	16.1	57.5	14.7	49.5	81.0	14.6	54.0	14.7	51.0	83.0	8.4	30.0	53.5
dext.	33.0	20.0	64.0	19.0	58.0	99.5	18.3	58.0	17.5	55.0	93.0	11.9	38.0	66.5
sin.	30.4	18.5	60.5	16.5	54.5	90.0	16.8	55.5	16.3	53.5	88.0	10.1	33.0	60.0
	23.6	14.0	59.3	12.0	50.8	85.7	12.5	53.0	14.0	59.3	100.0	7.9	33.5	63.2
	23.2	13.6	58.6	11.9	51.3	87.5	12.5	53.9	14.1	60.8	103.7	7.5	32.3	60.0

Table 1. A comparative table of metric values and indices of the first lower molar, M<sub>1</sub>, of the cave lion. Legend: 1) length of tooth crown; 2) length of protoconid; 3) length of paraconid; 4) width of tooth crown; 5) height of protoconid; 6) height of silon.

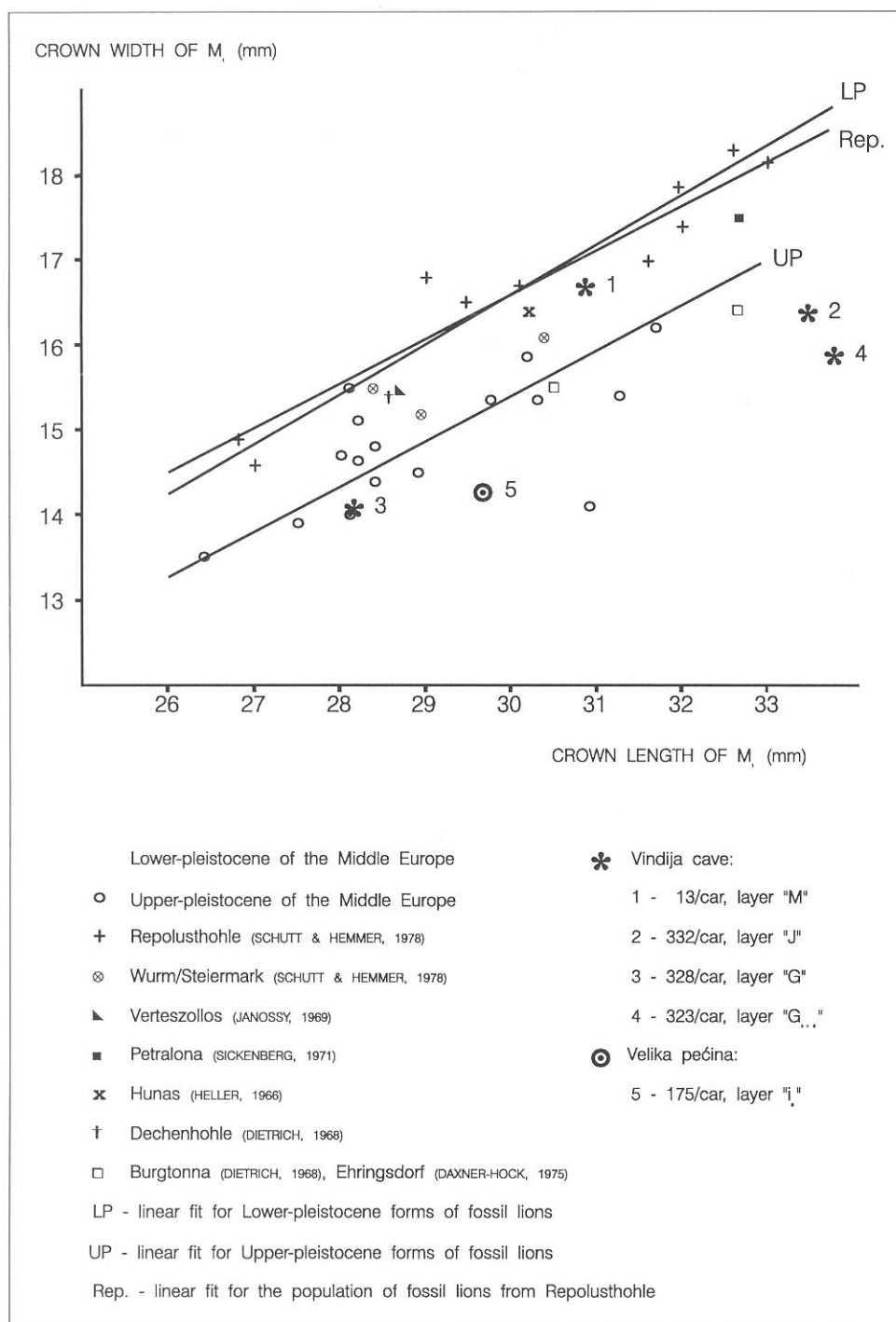


Fig. 4 Correlation of the first lower molar ( $M_1$ ) crown length and width of fossil lions.

the position of this tooth on the correlation diagrams (Figs. 4 & 5) which, together with the aforementioned characteristics, also indicates an Upper Pleistocene form of cave lion.

The first left lower molar, from the layer "G<sub>4+5</sub>" (323/car) of Vindija cave has a well-preserved tooth crown, but with a missing aboral root. At the buccal side, regular wearing can be observed. On the lingual side, the characteristic cingulum is divided by a recess into two parts. Almost all the indices calculated for this tooth (Table 1) indicate a more evolved Upper-Pleistocene form of cave lion. An exception is the index 2/1,

the value of which falls within the range of variation of the older form *Panthera leo fossilis* and the specific cave lion populations of Repolusthöhle. In view of other morphometric characteristics, and the known stratigraphical position, the possibility that this tooth belongs to the Middle and Lower Pleistocene forms of cave lion can be excluded. This is also confirmed by the position of the tooth on the correlation diagrams (Figs. 4 & 5).

The first right lower molar from the layer "G" of Vindija cave (328/car) has a well-preserved crown and a missing aboral root. Wearing at the buccal side of the crown is negligible, indicating that it was probably a

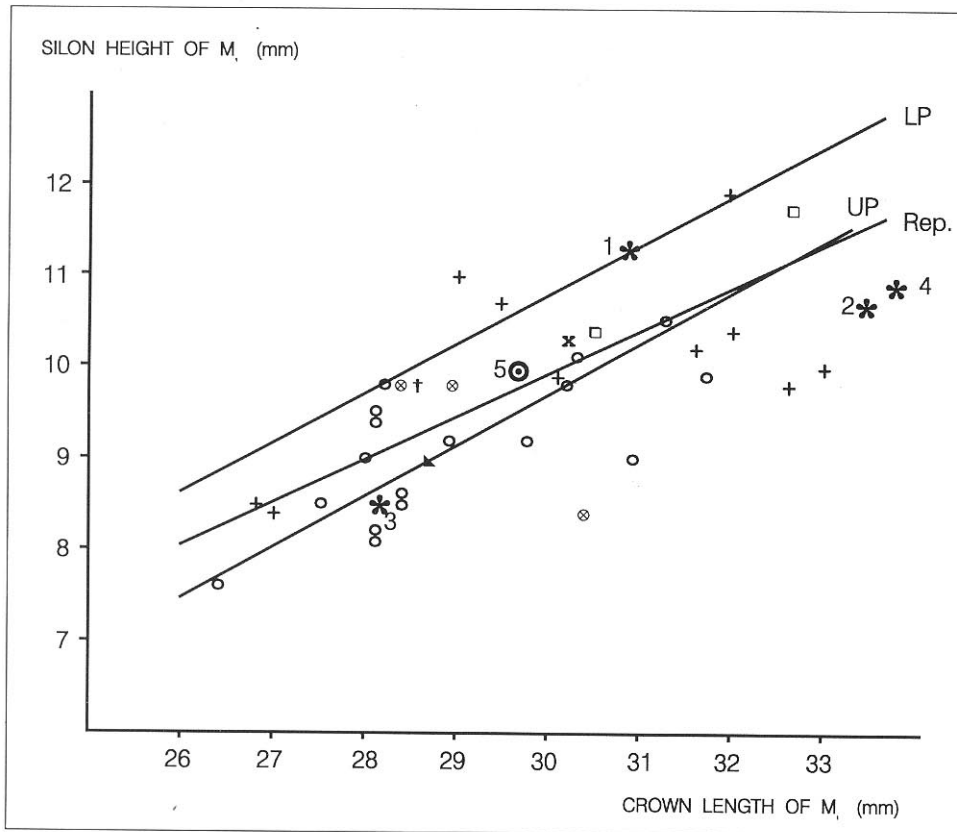


Fig. 5 Correlation of the first lower molar ( $M_1$ ) crown length and silon height of fossil lions (symbol descriptions as in Fig. 4).

younger adult individual. At first sight, small tooth dimensions are apparent but the determination of an adult individual is unquestionable. The thickened border of the crown base as well as the cingulum at the lingual side are well emphasised. The distribution of the indices of this tooth (Table 1) are very similar to the tooth from the layer "G<sub>4+5</sub>" (323/car). Most of the indices indicate an Upper Pleistocene form (some being extreme) while the index 2/1 suggests a similarity with the specific cave lion population from Repolusthöhle. The position of this tooth on the correlation diagrams (Figs. 4 & 5) confirms the determination of an Upper Pleistocene form of *Panthera spelaea*.

From the layer "i<sub>g</sub>" of Velika pećina the left lower jaw with preserved canine, P<sup>3</sup>, P<sup>4</sup> and M<sub>1</sub> (175/car) was separated (Fig. 1). At the buccal side of the first lower molar, considerable wearing is visible due to occlusion. The protoconid dominates over the paraconid, and at the lingual side, the cingulum is emphasised. The exceptionally high protoconid resulted in a 5/1 index (Table 1) indicative of older forms of cave lion, but, except for the non indicative ones, the indices 3/1, 4/1 and 6/1 clearly point to the fact that this tooth belongs to a younger Pleistocene form. It is necessary to point out that indices 2/1 and 3/2 point to metric characteristics similar to the Repolusthöhle population. The classification of this tooth as an Upper Pleistocene form of the species *Panthera spelaea* also confirms its position on the correlation diagrams (Figs. 4 & 5).

### 3.1.2. The fourth upper premolar - P<sup>4</sup>

The fourth right upper premolar from the layer "H" of the Vindija cave (317/car) is very well-preserved, missing only the oral branch of the root above the protocon. The paracon dominates over the metacon, and the protocon is well expressed on this tooth. At the lingual side the regular wearing by occlusion with M<sub>1</sub> is visible. According to the degree of wearing the tooth is supposed to have belonged to an adult individual. Except for the non-indicative ones, the indices 2/1, 5/4 and 8/1 (Table 2) point to a more evolved, respectively Upper Pleistocene form of *Panthera spelaea*.

From Vindija cave another fourth right upper premolar was separated, without layer marking (318/car). The paracon was damaged at the buccal side, its height being essentially reduced. The wearing of the metacon, paracon and also protocon is of a high degree which indicates an aged individual. All the three branches of the roots were well-preserved. The indices 2/1, 4/1, 5/4 and 8/1 (Table 2) are indicative of a Würmean form of *Panthera spelaea*.

A fourth upper left premolar (143/car) was separated from the layer "k" of Velika pećina. The tooth crown is well-preserved with visible irregular wearing at the lingual side. This wearing is of a high degree so that, on the paracon, there exists a visible opening of the pulp. The indices 2/1, 3/1, 5/4, 7/1 and 8/1 (Table 2) indicate a more evolved Upper Pleistocene form of cave lion.

	1 (mm)	2 (mm)	2/1 (%)	3 (mm)	3/1 (%)	4 mm	4/1 (%)	5 (mm)	5/1 (%)	5/4 (%)	6 (mm)	6/1 (%)	7 (mm)	7/1 (%)	8 (mm)	8/1 (%)	9 (mm)	9/1 (%)
<i>P. spelaea</i> , Vindija, 317/car, "H"	42.3	39.8	94.1	42.1	99.5	16.5	39.0	16.6	39.2	100.6	31.3	74.0	21.3	50.4	16.2	38.3	15.0	35.5
<i>P. spelaea</i> , Vindija, 318/car	39.7	36.4	91.7	-	-	13.9	35.0	15.6	39.3	112.2	29.3	73.8	-	-	13.9	35.0	14.1	35.5
<i>P. spelaea</i> , Veternica, 600/car, "f"	41.5	-	-	-	-	16.7	40.2	15.2	36.6	91.0	-	-	19.4	46.7	17.0	41.0	-	-
<i>P. spelaea</i> , Velika pećina, 143/car, "k"	36.3	34.6	95.3	35.1	96.7	13.5	37.2	14.1	38.8	104.4	27.2	74.9	17.2	47.4	13.4	36.9	11.6	32.0
<i>P. spelaea</i> sin.	41.3	40.0	96.8	40.8	98.7	15.7	38.0	15.5	37.5	98.7	31.3	75.7	23.0	55.6	17.6	42.6	16.1	38.9
<i>P. spelaea</i> dext. (ARGANT, 1991)	41.3	40.0	96.8	40.9	99.0	15.5	37.5	15.7	38.0	101.2	31.6	76.5	22.8	55.2	17.7	42.8	15.8	38.2
<i>P. mosbachensis</i> , Château (ARGANT, 1991)	40.7	39.5	97.0	-	-	15.8	38.8	14.9	36.6	94.3	31.0	76.1	-	-	14.6	35.9	14.8	36.4
<i>P. leo fossilis</i> min. value	36.4	35.5	95.5	36.4	98.5	14.0	37.0	13.8	36.0	92.0	27.3	72.5	18.3	49.0	14.0	38.5	13.0	35.5
<i>P. leo fossilis</i> max. value	45.1	42.6	97.5	44.9	100.0	17.5	40.0	16.8	39.5	98.0	32.7	76.0	21.7	52.0	17.3	39.5	17.8	40.0
<i>P. leo fossilis</i> av. value n=6	39.9	37.8	96.5	40.1	99.5	15.4	38.5	15.2	37.0	95.5	29.8	74.0	19.6	50.0	15.3	39.0	14.8	37.0
<i>P. leo spelaea</i> min. value	33.8	34.8	95.0	35.7	95.5	13.0	37.0	14.0	37.5	98.5	25.6	73.0	18.0	46.0	13.7	35.0	12.9	33.0
<i>P. leo spelaea</i> max. value	42.4	40.2	98.0	42.0	100.5	15.4	39.5	17.3	41.5	110.0	31.0	76.0	20.7	53.5	15.5	39.5	15.0	38.0
<i>P. leo spelaea</i> av. value n=7	38.4	37.6	96.0	38.7	99.0	14.5	38.5	15.3	40.0	103.0	28.7	74.5	19.1	50.0	14.7	37.5	13.9	35.5
Repolusthöhle min. value	40.3	39.0	97.0	40.3	100.0	16.0	39.5	16.0	39.5	99.5	30.9	76.5	20.7	50.0	15.6	38.0	14.0	34.5
Repolusthöhle max. value	41.4	41.2	99.5	41.6	100.5	16.8	40.5	16.7	40.5	100.0	32.0	77.5	21.4	53.0	16.4	39.5	15.0	36.5
Repolusthöhle av. value n=3	41.0	40.1	98.0	41.0	100.0	16.4	40.0	16.4	40.0	100.0	31.5	77.0	21.1	51.5	15.9	39.0	14.4	35.0
Würm, Steiermark min. value	38.0	36.2	91.5	36.6	94.5	14.3	36.0	14.5	38.0	99.0	28.4	73.0	18.3	47.5	13.7	34.0	13.0	35.0
Würm, Steiermark max. value	40.3	38.2	96.5	38.8	97.0	15.0	39.0	16.8	41.5	113.0	30.4	75.5	21.7	56.0	15.7	41.5	14.5	38.0
Würm, Steiermark av. value n=5	39.2	37.1	94.5	37.7	96.5	14.6	37.5	15.7	40.0	107.0	29.3	74.5	19.8	51.5	14.7	37.5	13.9	36.0

Table 2. A comparative table of metric values and indices of the fourth upper premolar, P<sup>4</sup>, of the cave lion. Legend: 1) exterior length of tooth crown; 2) length of crown in the middle of tooth; 3) interior length of tooth crown; 4) length of paracon; 5) length of metacon; 6) paracon + metacon length; 7) oral width of tooth crown; 8) aboral width of tooth crown; 9) minimal width behind talon.

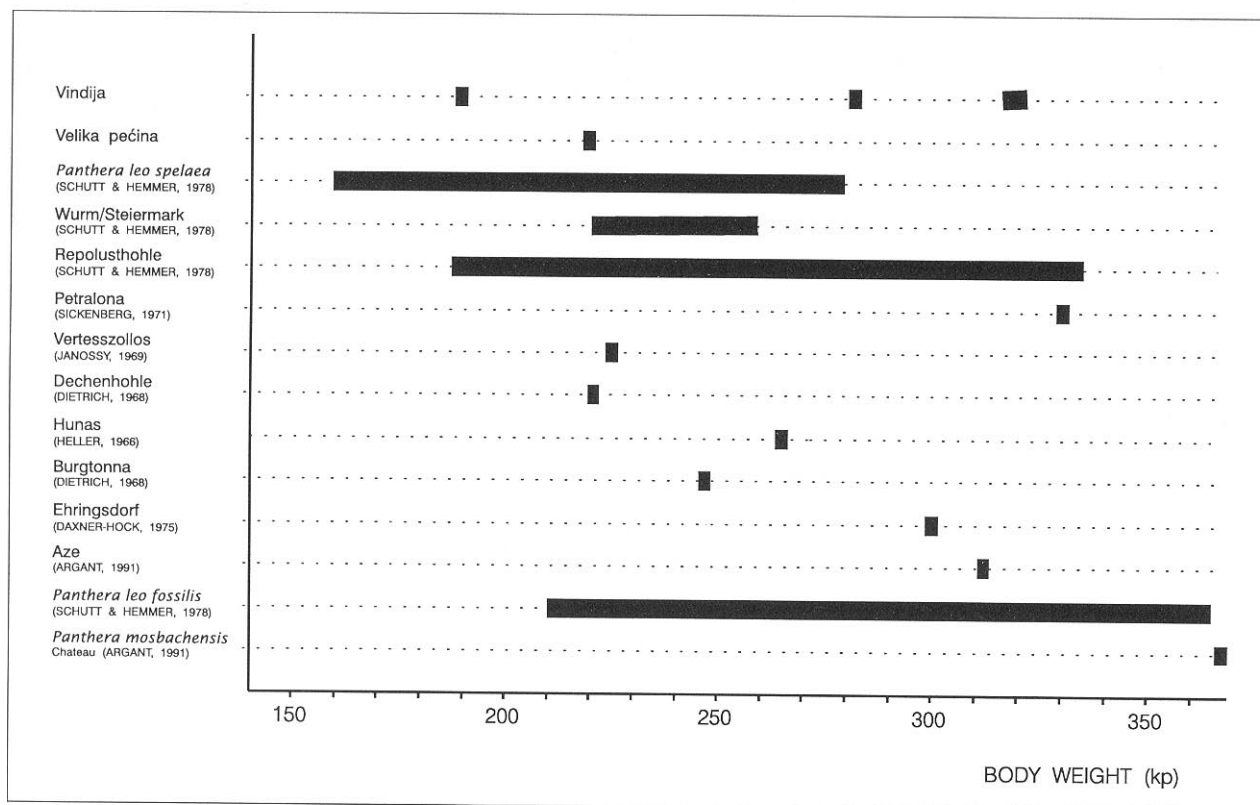


Fig. 6 Comparative diagram of fossil lion body weights from North-western Croatia and some other European sites.

### 3.2. ESTIMATION AND ANALYSIS OF BODY WEIGHTS

The body weight of individuals is an important palaeobiological characteristic, that also contributes to the knowledge on the variability of a given population. The values of body weights of the cave lion individuals from North-western Croatia, and the values and correlation for other groups and localities within Europe are shown on Fig. 6. As a general observation, stratigraphically older populations are characterised by larger body weights that can reach even 367 kp. The calculated indices (Tables 1 & 2) and known stratigraphic position, determine the cave lion population from North-western Croatia as belonging to the Middle and Upper Pleistocene, and although some teeth (from the layers 'M', 'J' and 'G<sub>4+5</sub>' of the Vindija cave) point to considerably higher body weights, (so that they exceed the maximum value for this species) the possibility of their belonging to older forms must be excluded. Some currently established characteristics of the cave lion population from North-western Croatia are also common to a specific population from Repolusthöhle, and are also supplemented by body weight analysis. However, the range of body weight values of the population from the North-western Croatia is completely enveloped by the variational range of the population from Repolusthöhle.

### 4. DISCUSSION AND CONCLUSIONS

The comparative analysis of the first lower molars of the cave lion from North-western Croatia indicates the presence of Middle and Upper Pleistocene forms of cave lion (Table 1). Some characteristics, close to those of the specific population from Repolusthöhle (Austria) by SCHÜTT & HEMMER (1978) were established on the teeth from layers "G<sub>4+5</sub>" and "G" of Vindija cave, and the layer "i<sub>g</sub>" from Velika pećina. It is indicative that all the three mentioned teeth have the same index (relation between protoconid length and tooth crown length) (Table 1) which points to a similarity with the Repolusthöhle population, and that all the mentioned teeth are in close stratigraphic relation (Würm 2/3, Würm 2). The result of the body weight analysis of the cave lion from North-western Croatia supplements the established common characteristics with the specific population from Repolusthöhle. The fact that the minimum and maximum body weights of the cave lion population from North-western Croatia were indicated by teeth which originated from the same layer ("G") of Vindija cave, supports the hypothesis of a high degree of the population heterogeneity. This also argues for the thesis on the heterogeneity of the populations of the European cave lions, and the impossibility of a global approach to the problem of the evolution of this species (SCHÜTT & HEMMER, 1978). Although the studied

teeth from the Upper Pleistocene of North-western Croatia cannot be identified with the specific population from Repolusthöhle, their characteristics clearly support SCHÜTT & HEMMER's (1978) thesis on separated lineages and the heterogeneity of the populations within cave lion lineages in the Europe. Considering some common characteristics of stratigraphically younger populations of the cave lion from North-western Croatia and the Repolusthöhle population it could be supposed that the Croatian populations belong to the West-European lineage with special characteristics, but confirmation of this hypothesis will be possible only after discoveries of new remains of this species.

## 5. REFERENCES

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