GEO&BIO

2026 • vol. 28, pp 49–68
https://doi.org/10.53452/gb2806

Cave lions (*Panthera spelaea*) of Ukraine: craniodental adaptations, morphometric comparisons, and evolutionary trends

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article info

key words

cave lion, African lion, skull, dentition, morphometric analysis

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article history

Submitted: 28.04.2026. Revised: 19.05.2026. Accepted: 20.05.2026

cite as

Velytchenko, Yu., & Kovalchuk, O. (2026). Cave lions (*Panthera spelaea*) of Ukraine: craniodental adaptations, morphometric comparisons, and evolutionary trends. *GEO&BIO*, *28*, 49–68. [English, with Ukrainian summary]

abstract

This article synthesizes osteological and craniodental evidence to reconstruct the evolutionary trajectory, functional morphology, and ecological significance of the cave lion *Panthera spelaea* in the territory of modern Ukraine. We examined a complete female skull from Kryshtaleva Cave, mandibular fragments from Kodak, and a male skull from Chernihiv, and compared them with systematically measured skulls of six captive African lions *Panthera leo*. To broaden the geographic and chronological context, published craniometric datasets for Ukrainian cave lion localities were incorporated, including Middle Pleistocene *Panthera spelaea fossilis*, putative *P. s. intermedia*, and Late Pleistocene *P. s. spelaea*. Standardised measurements of cranial, mandibular, and dental parameters were analysed separately by sex to account for pronounced dimorphism. Ukrainian cave lions show a consistent suite of adaptations linked to predation on megafauna under cold-steppe conditions: a shortened facial region and reduced diastema that increase mechanical advantage of the jaw; expansion of occipital and mastoid regions for powerful cervical and temporal musculature; enlarged nasal apertures suggesting climatic adaptation; and an odontological shift toward hypercarnivory. Dentition is characterised by robust, high canines, elongation and lateral compression of premolars, elongation of carnassial cutting blades, reduction of posterior molars, and shallower carnassial notches indicating specialization for slicing soft tissues rather than bone processing. Metric patterns also support a chronocline of size reduction from *Panthera spelaea fossilis* through intermediate forms to *Panthera spelaea spelaea* without loss of functional specialisation. The results refine morphological criteria for identifying cave lion remains from Ukraine and provide new insight into evolutionary trends within the genus *Panthera*.

Печерні леви (*Panthera spelaea*) України: краніодентальні адаптації, морфометричні порівняння та еволюційні тенденції

Юлія Велитченко, Олександр Ковальчук

Резюме. У цій статті проаналізовано краніодентальні параметри печерних левів *Panthera spelaea* за матеріалами з території України з метою реконструкції еволюційної траєкторії, функціональної морфології та екологічного значення виду. Ми дослідили повний череп самиці з Кришталевої печери, фрагменти нижньої щелепи з Кодака та череп самця з Чернігова і порівняли їх із відповідними параметрами черепів шести сучасних африканських левів *Panthera leo*, що утримувалися в неволі. Для розширення географічного та хронологічного контексту було включено опубліковані краніометричні набори даних для українських місцезнаходжень печерних левів, включаючи середньоплейстоценового *Panthera spelaea fossilis*, ймовірного *P. s. intermedia* та пізньоплейстоценового *P. s. spelaea*. Стандартизовані вимірювання параметрів черепа, нижньої щелепи та зубів були проаналізовані окремо за статтю, щоб врахувати виражений диморфізм. Печерні леви з території України демонструють послідовний набір пристосувань, пов'язаних із активним полюванням велику здобич в умовах тундростепу: вкорочена лицьова область та зменшена діастема, що збільшують механічну перевагу щелепи; розширення потиличної та соскоподібної областей для прикріплення потужної шийної і скроневої мускулатури; збільшені носові отвори, що свідчить про адаптацію до умов холодного клімату. Зубна система печерних левів характеризується високими іклами, видовженими і латерально стисненими премолярами, видовженими ріжучими лезами хижих зубів, зменшеними задніми молярами, що вказує на спеціалізацію на розрізанні м'яких тканин, а не на обробці (розгризанні) кісток. Отримані метричні параметри також підтверджують послідовне зменшення розмірів тіла від *Panthera spelaea fossilis* через проміжні форми до *Panthera spelaea spelaea* без втрати функціональної спеціалізації. Результати уточнюють морфологічні критерії для ідентифікації решток печерних левів із території України і надають нове розуміння еволюційних тенденцій у межах роду *Panthera*.

Ключові слова: печерний лев, африканський лев, череп, зубна система, морфометричний аналіз.

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Introduction

The cave lion (*Panthera spelaea* Goldfuss, 1810) represents one of the most iconic extinct members of the family Felidae. This species inhabited vast regions of Eurasia during the Pleistocene, including the territory of present-day Ukraine (Marciszak *et al*., 2023 and references therein). It is regarded as one of the largest feliform predators to have ever existed (Hemmer, 2003; Sotnikova & Nikolskiy, 2006; Diedrich, 2014a; Marciszak *et al*., 2019, 2020, 2023). Morphological distinctions, supported by genetic analyses, have confirmed that *Panthera spelaea* was a species separate from the modern African lion *Panthera leo* Linnaeus, 1758 (Barnett *et al*., 2009; Ersmark *et al*., 2015; de Manuel *et al*., 2020). The history of cave lion research in Ukraine dates back to the late nineteenth and early twentieth centuries, when the first fossil remains were found and described (Pidoplichko, 1956). Notable localities include Chernihiv, Kryshtaleva Cave, Kodak, Sambir, and other sites that have yielded unique osteological material (Marciszak *et al*., 2023). These finds are crucial for reconstructing the species' distribution and ecological role within the Pleistocene biocenoses of Eastern Europe.

The aim of this study is to determine the cranial anatomical features of cave lions from Ukraine and to conduct a morpho-functional comparison with modern African lions *Panthera leo*. This approach allows for a comparative assessment of cranial morphology between extinct and extant lions, thereby contributing to the understanding of their evolutionary divergence. In addition, it will help identify adaptations and evolutionary trends within the genus *Panthera*.

Materials and methods

The material examined in this study comprised fossil and modern representatives of the genus *Panthera* housed in the Department of Palaeontology, National Museum of Natural History

(NMNHU-P), National Academy of Sciences of Ukraine (Kyiv). Fossil specimens of the cave lion included a complete skull and mandible of a female from Kryshtaleva Cave (NMNHU-P OF-803/1964, OF-806/1964) and two mandibular fragments from Kodak (NMNHU-P OF-645/3197, OF-646/3541) (see Marciszak *et al*., 2023: Figs 3, 4). Comparative material of the modern lion (*Panthera leo*) consisted of six skulls originating from the Kyiv Zoological Park, of which two belonged to males (NMNHU-P 5991 (Fig. 1) and 6290 (Fig. 2)) and four to females (NMNHU-P 1120 (Fig. 3), 5584 (Fig. 4), 6003 (Fig. 5), 6020 (Fig. 6)). To expand the dataset and enable a comprehensive comparative analysis, published craniometric data of *P. spelaea* specimens from Ukraine were incorporated. These data, including information on locality, age, sex attribution, and metric parameters, were taken from Marciszak *et al*. (2023). The supplementary dataset comprised specimens from Sambir, Bilykh Stin Cave, Emine-Bair-Khosar, Molodova, Volia-Homulecka, Chernihiv, Kremenchuk, and Rudky.

Descriptions and measurements of cranial and dental material were conducted following standardised protocols. Measurement schemes and morphological terminology (Figs 7–12) were adopted directly from Marciszak *et al*. (2023), ensuring full methodological compatibility between original data and published records (Schmid, 1940; Argant, 2010). Measurements of lion specimens (skulls, mandible, teeth) are provided in Tables 1–4. Upper teeth are designated by capital letters (e.g., P4), whereas lower teeth are indicated in lowercase (e.g., p4).

Fig. 1. Skull and mandible of an extant adult male African lion, *Panthera leo* (NMNHU-P 5991). Scale bar: 50 mm.

Рис. 1. Череп і нижня щелепа дорослого самця африканського лева, *Panthera leo* (NMNHU-P 5991). Масштабний штрих: 50 мм.

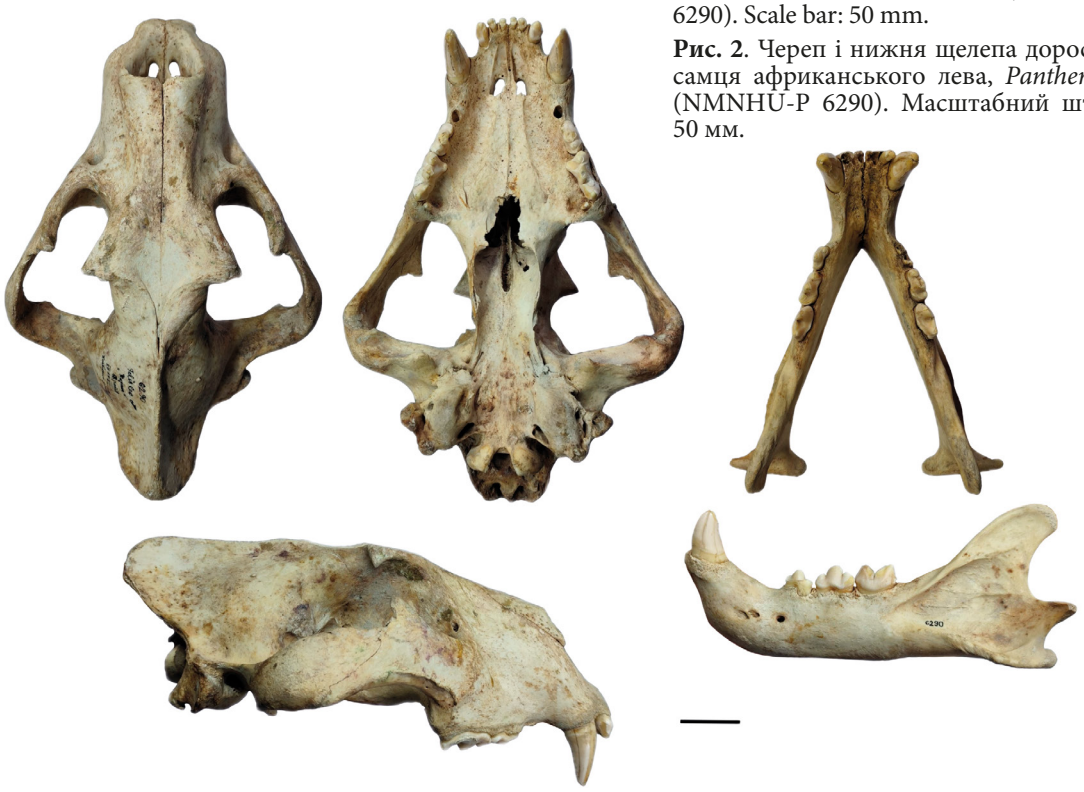

Fig. 2. Skull and mandible of an extant adult male African lion, *Panthera leo* (NMNHU-P 6290). Scale bar: 50 mm.

Рис. 2. Череп і нижня щелепа дорослого самця африканського лева, *Panthera leo* (NMNHU-P 6290). Масштабний штрих: 50 мм.

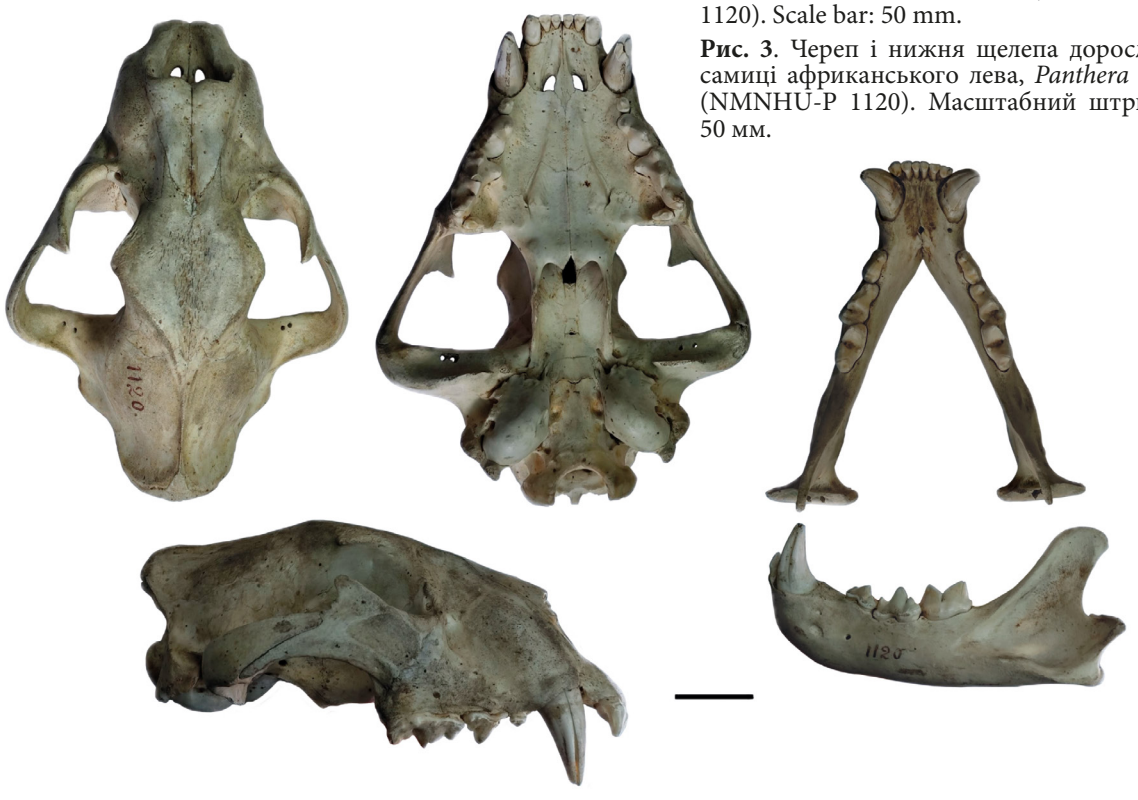

Fig. 3. Skull and mandible of an extant adult male African lion, *Panthera leo* (NMNHU-P 1120). Scale bar: 50 mm.

Рис. 3. Череп і нижня щелепа дорослої самиці африканського лева, *Panthera leo* (NMNHU-P 1120). Масштабний штрих: 50 мм.

Fig. 4. Skull of an extant adult male African lion, *Panthera leo* (NMNHU-P 5584). Scale bar: 50 mm.

Рис. 4. Череп дорослої самиці африканського лева, *Panthera leo* (NMNHU-P 5584). Масштабний штрих: 50 мм.

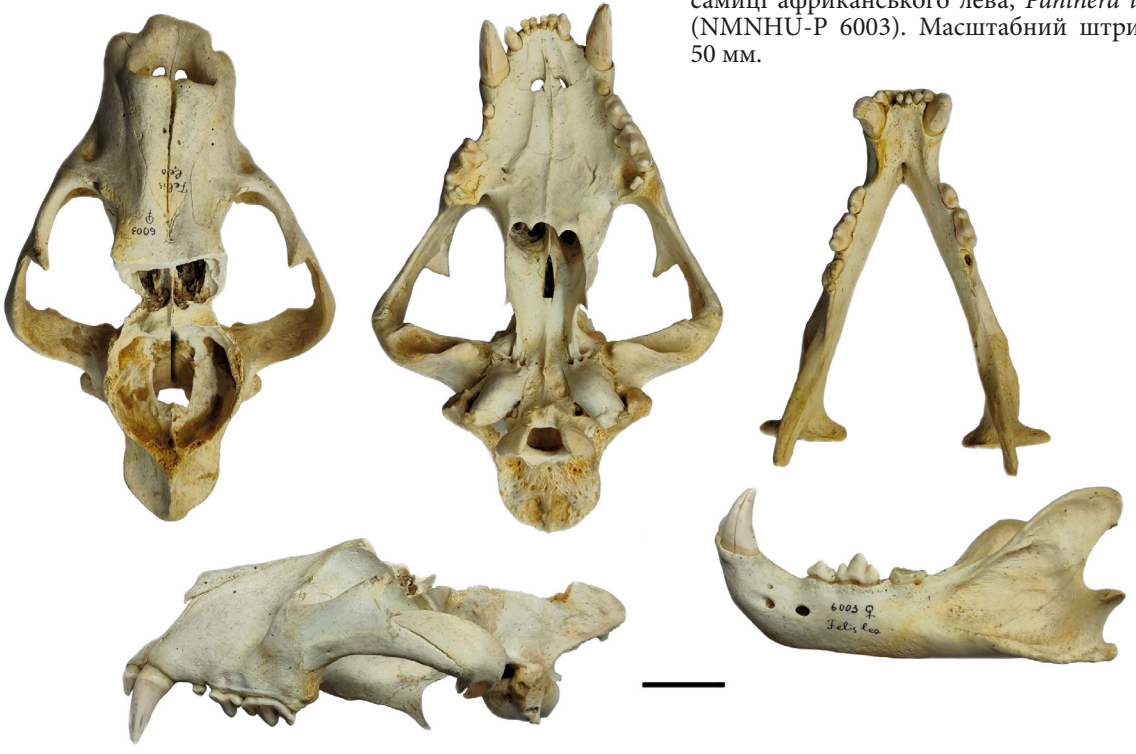

Fig. 5. Skull and mandible of an extant adult male African lion, *Panthera leo* (NMNHU-P 6003). Scale bar: 50 mm.

Рис. 5. Череп і нижня щелепа дорослої самиці африканського лева, *Panthera leo* (NMNHU-P 6003). Масштабний штрих: 50 мм.

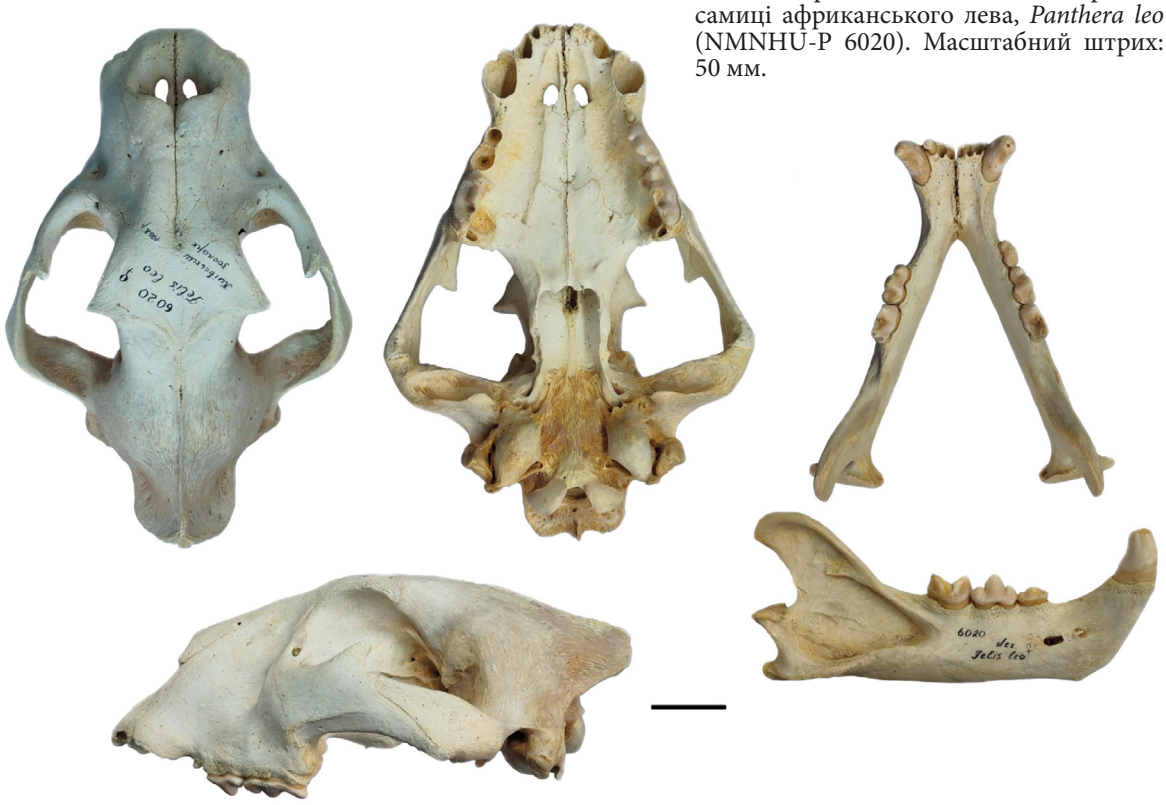

Fig. 6. Skull and mandible of an extant adult male African lion, *Panthera leo* (NMNHU-P 6020). Scale bar: 50 mm.

Рис. 6. Череп і нижня щелепа дорослої самиці африканського лева, *Panthera leo* (NMNHU-P 6020). Масштабний штрих: 50 мм.

Depending on specimen completeness, up to 40 parameters were recorded for the maxilla, up to 19 for the mandible, and 5–7 for each tooth. A differentiated measuring approach was applied to minimise instrumental error. Macro-measurements (e.g., total skull length, bizygomatic width) were taken using a standard calliper with a measuring range up to 50 cm. Micro-measurements (e.g., dental dimensions, alveolar lengths, and other fine-scale parameters) were obtained with an electronic calliper (range 15 cm; accuracy ±0.1 mm). In cases of damage to bone structures, the corresponding measurements were omitted and marked as "–" in tables.

Basic statistical processing of the dataset included calculation of arithmetic mean (M), as well as determination of variability limits (minimum, Min; maximum, Max). Given the pronounced sexual dimorphism characteristic of *Panthera*, statistical analyses were performed strictly separately for males and females of both species. Fossil specimens for which sex attribution was uncertain or not determined by previous authors were documented but excluded from mean-value calculations; they were used only to illustrate the metric range of the species.

Results and discussion

Fossil remains of cave lions are known from 42 localities across Ukraine (Marciszak *et al*., 2023: Fig. 1). Most finds derive from karstic cave systems in the west and south of the country. The assemblage particularly includes complete skulls, mandibular fragments, and isolated teeth. Two specimens have been attributed to *Panthera spelaea fossilis* (von Reichenau, 1906), three to probable *Panthera spelaea intermedia* Argant et Brugal, 2017, while the remainder are assigned to *Panthera spelaea spelaea* (Goldfuss, 1810).

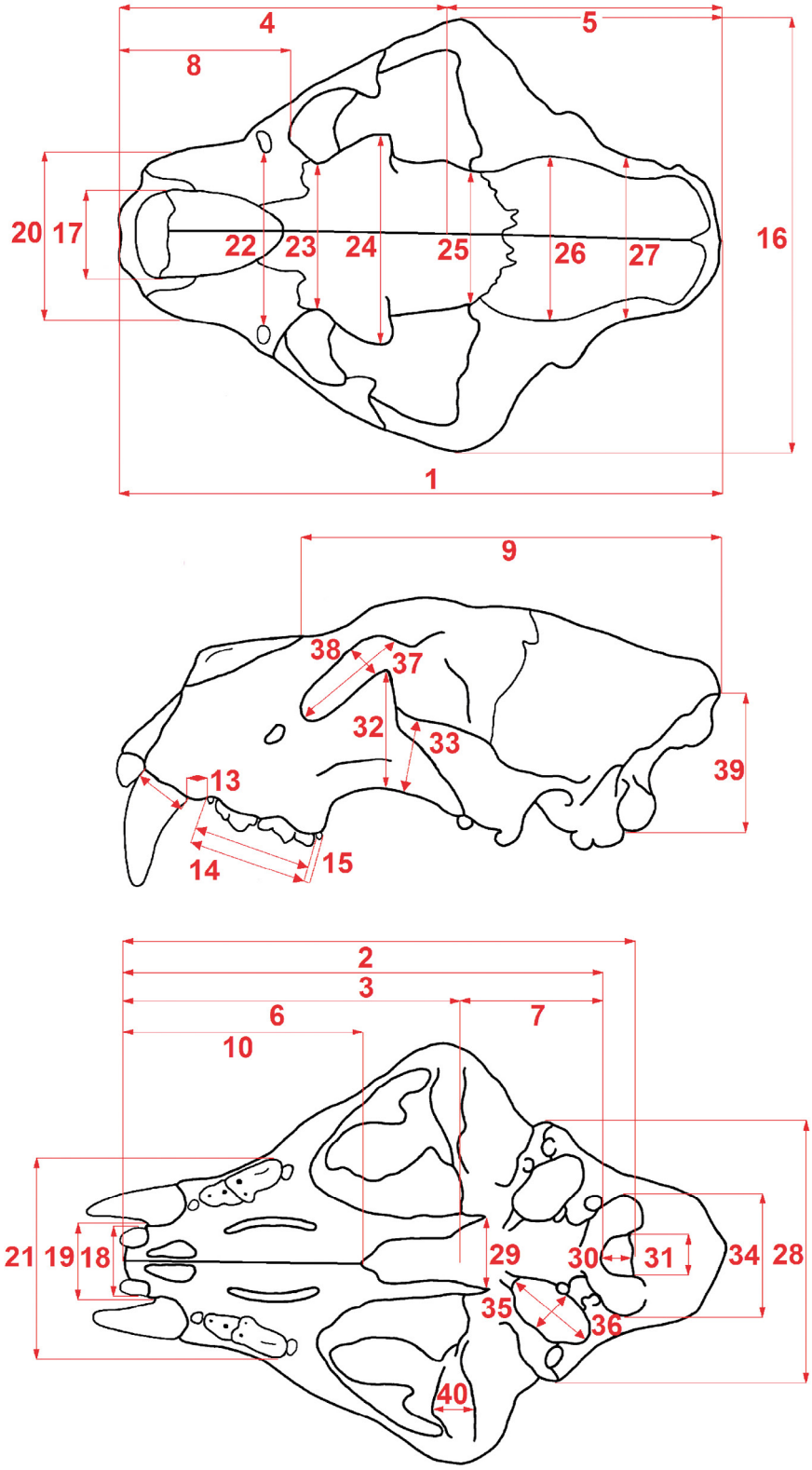

Fig. 7. Measurement scheme of the lion skull (adapted from Marciszak *et al.*, 2023). Measurement numbers correspond to those presented in Table 1.

Рис. 7. Схема промірів черепа лева (за: Marciszak *et al.*, 2023). Номери промірів відповідають таким у табл. 1.

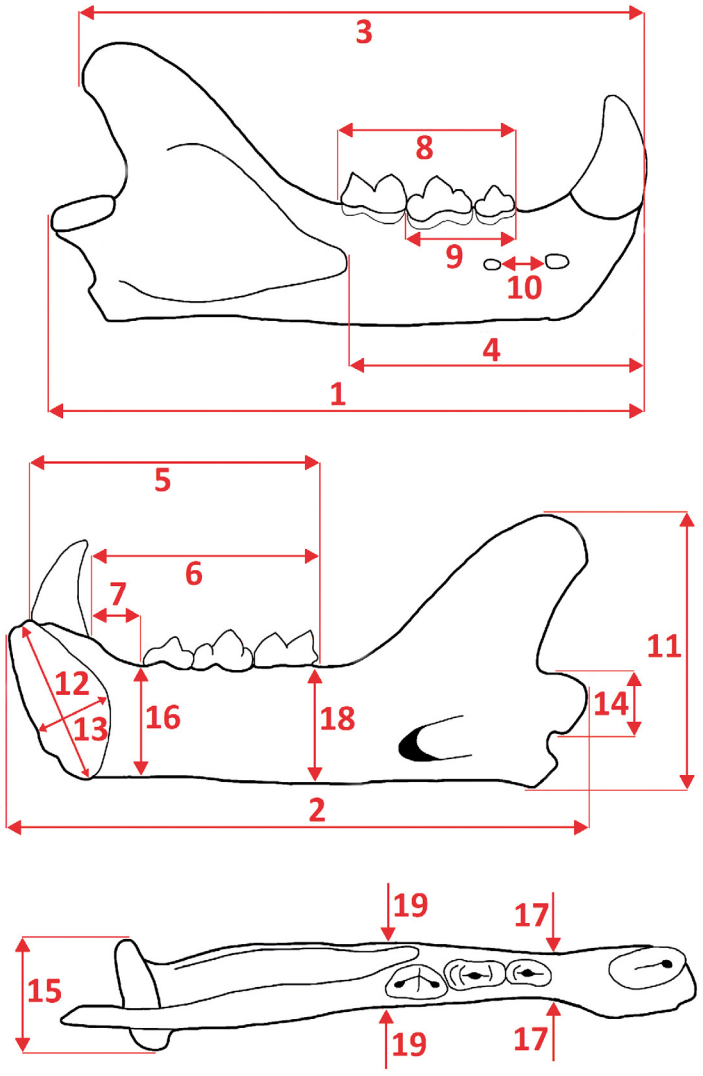

Fig. 8. Measurement scheme of the lion mandible (adapted from Marciszak *et al*., 2023). Measurement numbers correspond to those presented in Table 2.

Рис. 8. Схема промірів щелепи лева (за: Marciszak *et al*., 2023). Номери промірів відповідають таким у табл. 2.

Dentition of Panthera spelaea fossilis

Remains of *Panthera spelaea fossilis* have been recovered from two sites: Syniakove and Sambir. Both finds are dated to the Middle Pleistocene, with the Syniakove specimen more precisely constrained to c. 800–700 ka. Measurements of the lower first molar (m1) from Sambir indicate a male individual, as the tooth length exceeds 29 mm (Marciszak *et al*., 2023).

Morphologically, the tooth is larger than corresponding elements of *P. s. spelaea* and *P. leo*, confirming its attribution to *P. s. fossilis*. It exhibits a well-developed cingulum and talonid. The talonid, used for grinding food, was characteristic of earlier forms but became reduced in later cave lions as the cutting edge of the carnassial teeth evolved for slicing flesh more efficiently (Diedrich, 2014b). The robust cingulum likely protected the tooth against mechanical stress during predation on large prey. In contrast, smaller-bodied *P. s. spelaea* and modern *P. leo* targeted relatively smaller prey, reducing the need for such reinforcement (Van Valkenburgh, 2007; Marciszak & Gornig, 2024). The width-to-length ratio of m1 in *P. s. fossilis* is greater than in *P. s. spelaea*, indicating more massive dentition adapted to processing carcasses. Later cave lions evolved narrower, elongated teeth optimised for cutting rather than crushing, reflecting a dietary shift. These predators consumed flesh but avoided bone-cracking, leaving skeletal remains to scavengers such as cave hyenas *Crocuta crocuta spelaea*

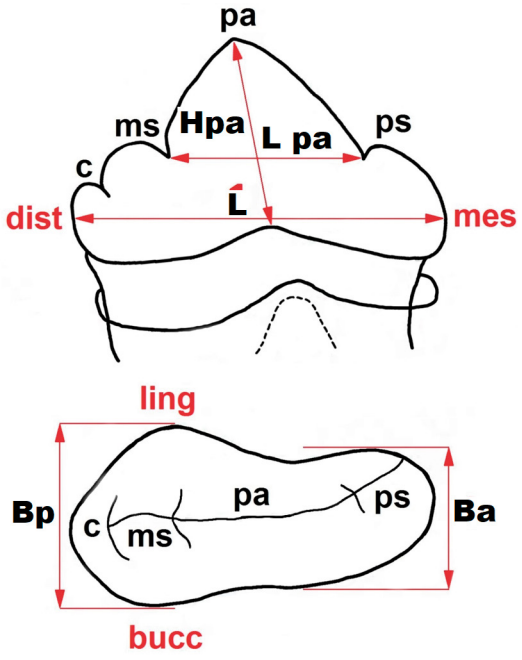

Fig. 9. Measurement scheme of the lion P3 (adapted from Marciszak *et al*., 2023): ps — parastyle, pa — paracone, ms — metastyle, c — cingulum (after Schmid, 1940); bucc — buccal, dist — distal, ling — lingual, mes — mesial. Measurement abbreviatiations correspond to those presented in Table 3.

Рис. 9. Схема промірів P3 лева (за: Marciszak *et al*., 2023): ps — парастиль, pa — паракон, ms — метастиль, c — цингулюм (за: Schmid, 1940); bucc — щічний, dist — дистальний, ling — лінгвальний, mes — мезіальний. Скорочення наведених промірів відповідають тим, що представлені в таблиці 3.

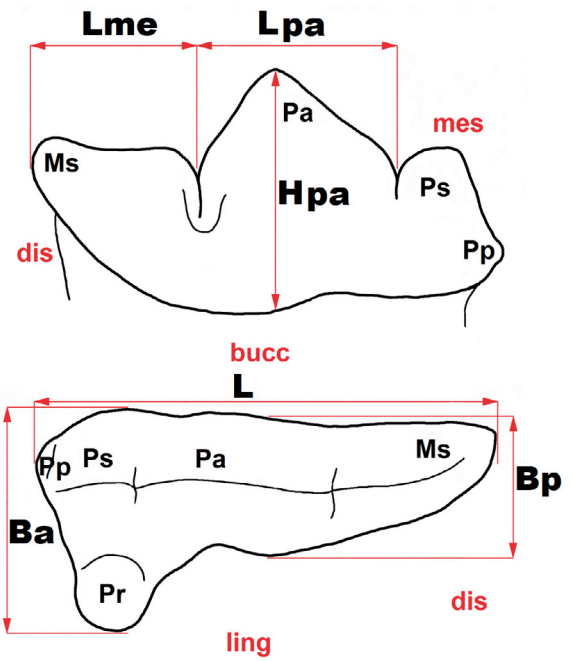

Fig. 10. Measurement scheme of the lion P4 (adapted from Marciszak *et al*., 2023): hy — hypocone, pp — preparastyle, pr — protocone, ps — parastyle, pa — paracone, me — metastyle, c — cingulum (after Scmid, 1940) ; bucc — buccal, dis — distal, ling — lingual, mes — mesial. Measurement abbreviatiations correspond to those presented in Table 3.

Рис. 10. Схема промірів P4 лева (за: Marciszak *et al*., 2023): hy — гіпокон, pp — препарастиль, pr — протокон, ps — парастиль, pa — паракон, me — метастиль, c — цингулюм (за: Schmid, 1940); bucc — щічний, dist — дистальний, ling — лінгвальний, mes — мезіальний. Скорочення наведених промірів таким у таблиці 3.

(Diedrich, 2014b). This supports the evolutionary trend of size reduction from the robust *P. s. fossilis* to the smaller *P. s. spelaea* (Van Valkenburgh, 2008; Marciszak & Gornig, 2024).

Interestingly, the width-to-length ratio of m1 in *P. s. fossilis* from Sambir is only slightly higher than in *P. leo*. In some individuals, the difference is minimal, suggesting that modern lions retain proportionally massive dentition despite hunting smaller prey. This reflects divergent evolutionary pathways: *Panthera leo* is a close relative but not a descendant of *P. spelaea*. The persistence of robust dentition in *P. leo* may be explained by ecological pressures in the African savanna, where lions face intense competition with other predators. Their teeth must withstand stress from feeding on smaller prey, including cartilage and bone fragments, necessitating durability (Van Valkenburgh, 2007, 2008; Barnett *et al*., 2009).

Comparative craniometric analysis of female cave lions from Ukraine and African lions

Skull and upper jaw (Table 1). The sample of female cave lions included specimens from Kryshtaleva Cave and Rudky, compared against female skulls of modern lions.

The Kryshtaleva Cave specimen exhibits clearly visible cranial sutures, indicating a juvenile individual. In large felids, cranial ossification follows a defined sequence, with sutures closing by 3–4 years of age in *P. leo* (White *et al*., 2026). Accordingly, reduced values in facial parameters (total and

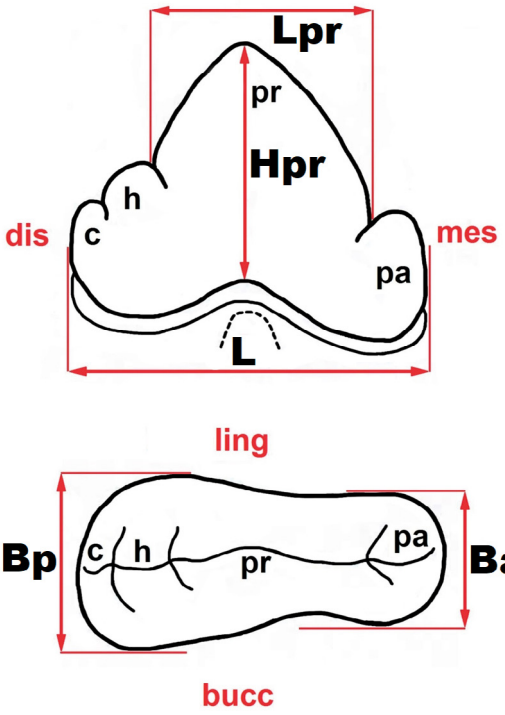

Fig. 11. Measurement scheme of the lion p3/p4 (adapted from Marciszak *et al*., 2023): pa — paraconide, pr — protoconide, h — hypoconide, t — talonid, c — cingulum (after Schmid, 1940) ; bucc — buccal, dist — distal, ling — lingual, mes — mesial. Measurement abbreviatiations correspond to those presented in Table 4.

Рис. 11. Схема промірів p3/p4 лева (за: Marciszak *et al*., 2023): pa — параконід, pr — протоконід, h — гіпоконід, t — талонід, c — цингулюм (за: Schmid, 1940); bucc — щічний, dist — дистальний, ling — лінгвальний, mes — мезіальний. Скорочення промірів відповідають таким у таблиці 4.

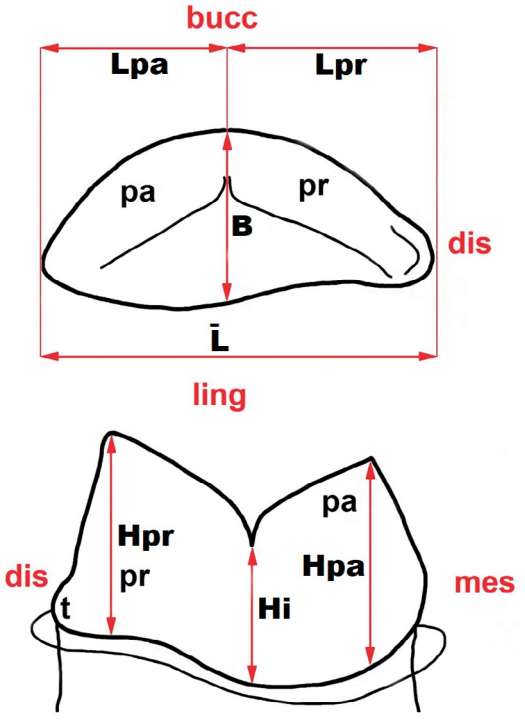

Fig. 12. Measurement scheme of the lion m1 (adapted from Marciszak *et al*., 2023): pa — paraconide, pr — protoconide, h — hypoconide, t — talonid, c — cingulum (after Schmid, 1940); bucc — buccal, dist — distal, ling — lingual, mes — mesial. Measurement abbreviatiations correspond to those presented in Table 4.

Рис. 12. Схема промірів m1 лева (за: Marciszak *et al*., 2023): pa — параконід, pr — протоконід, h — гіпоконід, t — талонід, c — цингулюм (за: Schmid, 1940); bucc — щічний, dist — дистальний, ling — лінгвальний, mes — мезіальний. Скорочення промірів відповідають таким у таблиці 4.

basifacial length, visceral skull length, rostrum, palate, diastema, and muzzle width indices) reflect incomplete ontogenetic development rather than evolutionary reduction. These features are consistent with allometric growth patterns in mammals, where the facial skeleton continues to elongate until full maturity. The underdeveloped zygomatic arches further suggest that the masticatory musculature had not yet reached adult volume, as zygomatic expansion parallels muscle growth (Slater & Van Valkenburgh, 2009; Segura *et al*., 2016).

Despite facial immaturity, the neurocranial and basal regions of the Kryshtaleva specimen already exceed mean values of adult *Panthera leo* females (Table 1). Greater basicranial length, cranial height, and enlarged auditory bullae suggest relatively larger braincase dimensions and potentially enhanced auditory capacity in *P. spelaea*. The broad frontal region and widely spaced orbits, producing a flat forehead, are characteristic features of cave lions. Importantly, the length of the upper premolar row (fixed after tooth eruption) already surpasses that of *Panthera leo*, indicating a more robust dental apparatus. The maximum width of the mandibular fossa also exceeds modern lion averages, implying a temporomandibular joint capable of generating high bite forces, consistent with predation on large prey (Meachen-Samuels & Van Valkenburgh, 2009; Slater & Van Valkenburgh, 2009; Segura *et al*., 2016).

Table 1. **Cranial measurements (mm) of** *Panthera spelaea spelaea* **from Kryshtaleva Cave (Ukraine) compared with extant** ***Panthera leo.*** Measurement numbers (first column) correspond to those shown in Figure 1.

Таблиця 1. **Проміри черепа (у мм)** ***Panthera spelaea spelaea*** **з печери Кришталева (Україна) у порівнянні з сучасними представниками** ***Panthera leo.*** Номери промірів (перший стовпець) відповідають тим, що наведені на рис. 1.

		Panthera spelaea spelaea (Goldfuss, 1810)	*Panthera leo* Linnaeus, 1758 (extant)					
	Inventory number (NMNHU-P)	OF-803/1964	6290	5991	6003	5584	1120	6020
	Sex	♀	♂	♂	♀	♀	♀	♀
1	Total length	292.0	378.3	384.0	290.0	310.5	282.0	319.0
2	Condylobasal length	269.8	334.5	338.0	249.0	279.2	262.0	284.5
3	Basal length	250.0	317.6	324.5	229.0	263.5	244.8	265.3
4	Viscerocranium length	173.0	237.0	235.0	170.5	195.5	183.0	192.0
5	Neurocranium length (point F–acrocranion)	117.0	141.5	158.0	130.5	114.5	105.0	122.0
6	Basifacial length	175.3	234.0	234.0	168.0	189.5	175.0	204.5
7	Basicranial length	78.5	84.0	91.0	60.0	76.5	70.8	61.5
8	Rostrum length	103.0	143.0	130.0	105.0	116.0	105.0	116.0
9	Neurocranium length (nasion–basion)	185.0	225.3	233.0	165.0	183.0	168.5	189.2
10	Palatal length	132.2	168.0	170.5	121.0	144.0	133.5	150.4
11	C1–M1 external length on alveoli	97.0	120.0	112.6	91.5	99.5	97.5	105.9
12	C1–M1 internal length on alveoli	79.0	101.1	92.5	75.1	84.5	81.0	80.2
13	Diastema length	4.7	17.1	12.0	11.3	13.7	5.7	11.7
14	Upper tooth row length on alveoli	70.7	80.5	74.3	65.5	67.0	73.7	72.3
15	Upper premolars row length	69.2	77.1	72.0	60.2	66.3	71.3	69.3
16	Breadth at zygomatic arches	189.0	257.0	249.0	195.0	203.5	207.2	219.0
17	Nasal aperture breadth	42.5	50.1	50.2	41.2	51.5	47.0	59.8
18	Maximum incisor row breadth at alveolus (I3–I3 breadth)	41.3	51.1	46.4	40.4	50.7	45.0	56.8
19	Minimum breadth between canines at internal margins of canine alveolus	50.0	65.2	60.8	50.0	65.1	51.5	58.5
20	Maximum breadth between canines at external margins of canine alveolus	89.9	98.8	106.5	78.5	86.3	90.5	94.3
21	Maximum palatal breadth at P4 external alveoli	115.0	113.0	123.0	89.0	105.0	109.0	121.0
22	Least distance between infraorbital foramina	85.6	91.0	100.0	72.5	83.7	82.5	86.3
23	Least distance between orbits	69.8	72.0	78.3	53.0	61.2	55.4	67.0
24	Frontal breadth	90.2	110.9	124.2	–	95.7	82.2	103.3
25	Postorbital least breadth	61.3	63.5	73.0	–	61.6	67.5	64.0
26	Maximum neurocranium breadth	85.0	97.0	94.0	82.0	85.5	85.5	93.0
27	Least breadth at parieto–temporale suturae	73.0	74.0	75.0	57.5	62.3	73.0	65.5
28	Mastoid breadth	118.2	153.0	150.0	111.3	113.5	121.7	128.0
29	Minimum breadth between pterygoids	32.5	45.0	36.5	41.0	31.7	38.0	34.0
30	Height of foramen magnum	19.5	15.5	17.3	21.5	18.3	18.5	18.5
31	Breadth of foramen magnum	26.5	28.3	30.0	28.0	29.7	34.3	32.3
32	Maximum height of zygomatic arch	46.5	54.5	63.5	44.5	52.3	45.5	48.0
33	Minimum height of zygomatic arch	29.5	38.2	34.5	27.0	28.5	23.0	28.7
34	Maximum breadth of occipital condyli	58.0	56.7	60.0	50.3	56.3	62.8	58.9
35	Tympanic bullae length	44.0	47.7	52.2	38.3	40.7	46.3	41.0
36	Tympanic bullae breadth	30.4	27.3	29.0	20.5	20.5	30.0	27.7
37	Maximum length of orbit	60.0	65.7	75.5	53.0	67.0	54.3	60.0
38	Maximum height of orbit	49.0	55.1	55.3	45.5	51.5	55.0	51.5
39	Cranial height (acrocranion–basion)	78.0	105.0	80.0	68.5	61.5	86.0	91.0
40	Maximum breadth at cavitas glenoidea	21.5	20.0	24.5	14.5	17.4	18.5	18.0

The adult Rudky specimen demonstrates the true species-level proportions of *Panthera spelaea*. Its minimal postorbital constriction, mastoid process width, and maximum width between occipital condyles significantly exceed those of modern lionesses. These expansions provided increased surface area for attachment of cervical and temporal musculature, biomechanically adapted for powerful

biting and large prey retention (Radinsky, 1981; Meachen-Samuels & Van Valkenburgh, 2009; Sicuro & Oliveira, 2011). By contrast, the juvenile Kryshtaleva specimen shows intermediate values, reflecting incomplete muscular development at the time of death. It is noteworthy that captive lions often display cranial modifications due to diet and reduced physical exertion, including broader zygomatic arches, shorter skull length, and reduced cranial cavity volume (Cooper *et al*., 2023). Thus, the mean values of *P. leo* in this study may be artificially elevated by zoo-derived specimens.

Lower jaw (Table 2). The sample of mandibles of cave lionesses derives from the sites of Kryshtaleva Cave, Rudky, and Molodova. Despite the likely differences in ontogenetic stage among the individuals represented, the metric data are similar. Most linear parameters of the mandible in the cave lionesses are smaller than the mean values recorded in modern African lionesses. This group includes the total length of the mandible, the distances from infradentale to the coronoid, angular processes and masseteric fossa, and the length of the diastema.

Table 2. Mandibular measurements (mm) of *Panthera spelaea spelaea* from Ukraine compared with extant *Panthera leo*. Measurement numbers (first column) correspond to those shown in Figure 2.

Таблиця 2. Проміри нижньої щелепи (у мм) *Panthera spelaea spelaea* з України у порівнянні з сучасними представниками *Panthera leo*. Номери промірів (перший стовпець) відповідають тим, що наведені на рис. 2.

		Panthera spelaea spelaea (Goldfuss, 1810)		*Panthera leo* Linnaeus, 1758 (extant)				
		Kryshtaleva Cave	Kodak					
	Inventory number	OF-806/1964	OF-646/3541	6290	5991	6003	1120	6020
	Sex	♀	♂	♂	♂	♀	♀	♀
1	Total length	196.5	–	255.0	260.0	206.5	190.0	218.5
2	Length from infradentale to angular process	193.0	–	250.0	266.5	202.0	197.0	222.7
3	Length from infradentale to coronoid process	194.5	–	252.0	268.0	205.0	195.0	223.2
4	Length from infradentale to mesial margin of masseteric fossa	108.5	–	145.0	131.0	117.0	110.0	118.0
5	c1–m1 external length	110.7	130.2	139.0	133.5	107.0	112.0	126.3
6	c1–m1 internal length	93.5	107.5	119.0	108.0	87.7	92.0	103.5
7	Length of diastema	20.0	21.3	39.5	34.7	27.0	19.5	38.5
8	Length of the cheek teeth row	67.7	74.7	77.0	70.5	61.3	72.3	68.0
9	Length of the premolars row	43.1	47.8	49.0	44.5	39.4	47.8	43.5
10	Smallest distance between mental foramina	14.6	13.6	12.0	15.4	10.8	12.5	7.2
11	Ramus height	89.2	–	111.3	123.4	88.0	88.3	93.6
12	Symphysis maximum diameter	–	–	–	–	–	–	79.0
13	Symphysis minimum diameter	–	35.0	–	–	–	–	28.5
14	Condyle height	16.7	–	16.8	20.2	11.6	17.5	16.3
15	Condyle breadth	42.4	–	60.8	56.3	50.7	51.3	49.9
16	Mandibular body height before p3	38.5	56.1	49.6	50.6	37.0	44.7	43.4
17	Mandibular body thickness before p3	17.2	26.1	20.1	22.1	15.4	20.5	18.0
18	Mandibular body height behind m1	43.0	51.4	53.0	53.0	41.5	44.3	49.3
19	Mandibular body thickness behind m1	20.2	26.6	22.7	22.5	18.8	18.8	22.2

The mandibular body is also less robust: the height and thickness of the bone anterior to p3 and posterior to m1, together with the diameter of the symphysis and the width of the condylar process, are all reduced compared with *P. leo*. Since the specimen from Rudky has been identified as an adult individual, the general shortening and gracility of the mandibular body cannot be explained solely by juvenile age (as in the case of the Kryshtaleva Cave specimen). This indicates that the shortened mandible was a species-level (or possibly sex-linked) norm among Late Pleistocene cave lionesses of the region (Marciszak *et al*., 2023). From a biomechanical perspective, such shortening represents an evolutionary advantage, as it brings the cutting tooth complex and canine closer to the temporomandibular joint. According to biomechanical principles, the smaller the distance between the

point of force application (tooth) and the fulcrum (joint), the greater the bite pressure generated. Thus, the mandible of *P. spelaea* was shorter yet more powerful, producing a stronger bite than the elongated mandible of modern lionesses (Therrien, 2005).

Despite the overall shortening of the mandible, the length of the cheek-tooth row (p3–m1) in cave lionesses exceeds the mean value in modern lionesses. An extended cheek-tooth row combined with reduced overall mandibular length and shortened diastema indicates a high density of tooth placement. This contrast in parameters exemplifies mosaic evolution during the general diminution of the species. It is well established that Late Pleistocene *Panthera spelaea spelaea* underwent evolutionary size reduction compared with their large Middle Pleistocene ancestors (*P. s. fossilis*). In such evolutionary processes, skeletal structures adapt relatively rapidly, whereas odontological parameters are highly conservative and change with evolutionary delay. Since large teeth remained essential for slicing the flesh of megafauna, the dentition was not reduced proportionally to the shrinking mandibular bone but retained functional strength. This produced a dense, massive cutting row on a relatively gracile mandible, a hallmark of hypercarnivory — specialisation in meat consumption and the need for rapid processing of prey (Van Valkenburgh, 1989; Marciszak & Gornig, 2024).

Parameters that proved larger in cave lionesses than in modern lionesses include the height of the condylar process and the minimum distance between the mental foramina. The condylar process forms the temporomandibular joint with the skull. Increased height alters the spatial position of the joint relative to the tooth row and modifies the angle of attachment of the masseter and temporalis muscles, thereby increasing their leverage. This compensates for the shortened mandible: even with a relatively slender mandibular bone, the elevated condylar process enabled cave lions to generate considerable compressive force, essential for killing large prey. The reduced width of the process combined with its great height indicates optimisation of the mandible for vertical movements and resistance to tensile stresses, while lateral (chewing) movements were minimised (Van Valkenburgh, 1989; Therrien, 2005).

The mental foramina transmit nerves and blood vessels supplying sensitivity and vascularisation to the tissues of the lower muzzle, including the lower lip and canine region. Greater distance and probably a wider canal may reflect an expanded zone of innervation, potentially linked to enhanced muzzle sensitivity and improved sensory capacity (possibly through vibrissae or other tactile specialisations). In assessing the gracility of the mandibular body (its height and thickness), one must consider the provenance of the modern comparative sample from a zoological park. The absence of natural mechanical stresses (struggle with prey, tearing of tough tissues) in captivity leads to lifetime modification of bone tissue, often rendering zoo lions' mandibles less robust than those of their wild counterparts. Yet even against the background of potentially weaker mandibles in the modern sample, *P. spelaea* specimens display greater skeletal gracility. At the same time, their dentition (unaffected by diet) retains large dimensions. This further supports the interpretation of mosaic evolution in the species, whereby a specialised, massive dentition functioned upon a relatively shortened and lightened bony foundation (Cooper *et al*., 2023). Morphometric analysis of the mandible confirms the specialisation of *Panthera spelaea* for hypercarnivory. The general shortening and gracility of the mandible in lionesses resulted from evolutionary diminution of the species, yet owing to the conservatism of the dentition they retained a massive cheek-tooth row. Moreover, a shorter mandible with an elevated condylar process allowed generation of high bite force, necessary for hunting representatives of the Pleistocene megafauna. Modern *P. leo* possess proportionally longer and thicker mandibles with a relatively smaller cutting block, reflecting adaptation to a more generalist diet in the savanna environment.

Upper dentition (Table 3). Analysis of the upper dentition of cave lionesses (specimens from Kryshtaleva Cave, Rudky, and Molodova) reveals consistently larger canines in both width and height compared to modern lionesses (Table 3). These teeth functioned as primary weapons for grasping and delivering fatal bites, with increased basal robustness preventing fracture under lateral stress during struggles with large prey (Meachen-Samuels & Van Valkenburgh, 2009).

The relatively large second premolar (P2) reflects the general robustness of the maxilla and correlates with a broad anterior dental row, enhancing prey retention. In contrast, modern lions, adapted to smaller prey, exhibit less massive dentition (Van Valkenburgh, 1989).

Table 3. **Upper teeth measurements (mm) of *Panthera spelaea spelaea* from Kryshtaleva Cave (Ukraine) compared with extant *Panthera leo.***

Таблиця 3. **Проміри верхніх зубів (у мм) *Panthera spelaea spelaea* з Кришталевої печери (Україна) у порівнянні з сучасними представниками *Panthera leo.***

Tooth	Inventory number / Sex	*Panthera spelaea spelaea* OF-803/1964 ♀	*Panthera leo* Linnaeus, 1758 (extant) 6290 ♂	5991 ♂	6003 ♀	5584 ♀	1120 ♀	6020 ♀
I1	Total length (L)	–	7.7	5.7	6.0	6.4	8.0	–
	Total width (B)	–	5.5	5.7	4.5	4.7	5.5	–
	Total height (H)	–	7.6	9.0	7.0	6.1	9.4	–
I2	Total length (L)	–	8.5	9.1	7.0	–	10.0	–
	Total width (B)	–	7.2	6.6	5.8	–	6.6	–
	Total height (H)	–	9.0	10.0	8.7	–	11.1	–
I3	Total length (L)	–	13.0	14.5	10.8	11.2	13.0	–
	Total width (B)	–	10.8	10.5	8.5	8.8	10.0	–
	Total height (H)	–	15.8	16.8	14.5	13.2	16.7	–
C1	Total length (L)	19.0	20.6	22.0	17.0	18.5	20.0	–
	Total width (B)	15.0	16.6	19.0	14.7	13.2	14.2	–
	Total height (H)	46.5	42.5	58.0	38.0	35.4	48.3	–
P2	Total length (L)	8.6	–	5.5	7.7	8.2	9.0	5.1
	Total width (B)	5.9	–	4.3	6.4	6.6	7.0	4.3
	Total height (H)	5.3	–	6.0	5.9	5.0	6.4	4.2
P3	Total length (L)	24.0	25.1	27.0	20.0	20.3	26.7	24.6
	Paracone length (L pa)	12.5	11.3	12.4	10.0	9.5	11.7	11.2
	Paracone height (H pa)	13.3	–	16.4	13.8	11.5	15.6	14.8
	Mesial breadth (Ba)	10.0	9.2	11.0	10.0	8.5	11.2	11.2
	Distal breadth (Bp)	10.0	12.0	15.0	11.0	10.7	15.8	12.8
P4	Total length (L)	35.5	36.6	35.0	29.7	31.8	37.9	35.6
	Paracone length (L pa)	12.9	14.0	15.3	12.0	12.5	15.0	13.5
	Paracone height (H pa)	17.7	18.0	20.0	18.1	13.4	21.4	17.8
	Metastyle length (L me)	14.1	13.0	13.6	11.0	11.8	14.5	13.8
	Mesial breadth (Ba)	18.0	18.4	19.3	15.4	16.0	20.3	18.0
	Distal breadth (Bp)	12.0	10.5	13.2	9.8	12.0	15.4	13.2
M1	Total length (L)	9.5	9.7	8.7	9.0	12.0	14.2	8.8
	Total width (B)	–	6.0	5.0	4.4	–	6.4	–
	Total height (H)	–	2.6	4.3	3.5	–	4.0	–

The third premolar (P3) in cave lionesses shows evolutionary elongation and narrowing. Although overall tooth length and paracone length (Lpa) are greater than in *P. leo*, distal width (Bp) is reduced. This transformation produced a blade-like morphology optimised for cutting, complementing the carnassial (P4). In modern lionesses, P3 is typically broader posteriorly, allowing limited crushing of cartilage or small bones (Van Valkenburgh, 1989, 2007, 2008). Cave lion P3 morphology thus reflects specialisation towards hypercarnivory, with reduced emphasis on bone processing (Bocherens *et al.*, 2011; Marciszak & Gornig, 2024).

An analogous evolutionary trend is confirmed by the proportions of the upper carnassial (P4). The overall length of P4 in cave lionesses exceeds the mean values of modern lionesses. However, internal proportions differ: the paracone (anterior cusp) is shorter than in *P. leo*, while the metastyle (Lme) is markedly elongated. Functionally, the extended metastyle worked in tandem with the protoconid of the lower carnassial (m1), forming the principal cutting complex for slicing flesh. This elongation represents a specialisation of the dental apparatus for rapid and efficient meat processing. The reduction of the paracone is a direct consequence of metastyle elongation. In modern lions, P4 is typically shorter and broader, allowing occasional crushing of cartilage and small bones. By contrast, cave lions were specialised for cutting soft tissues, reflected in their elongated tooth morphology (Van Valkenburgh, 1989, 2007, 2008).

The first upper molar (M1) in fossil specimens is smaller than the mean values of modern lionesses. In felids, M1 is a rudimentary structure, derived from grinding teeth but now positioned transversely and largely functionless. Felid evolution is characterised by progressive reduction of posterior molars in favour of an enlarged carnassial complex. The further reduction of M1 in *P. spelaea* confirms its status as a hypercarnivore, with a diet focused on flesh rather than tough tissues (Van Valkenburgh, 1989, 2007). Dental metrics are genetically determined and unaffected by captivity or diet. Thus, odontometric differences between *P. spelaea* and *P. leo* provide reliable indicators of species-level divergence (Cooper *et al*., 2023).

Odontometric analysis of the upper jaw demonstrates that the dentition of *P. spelaea* evolved towards hypercarnivory (Bocherens *et al*., 2011; Marciszak & Gornig, 2024). Enlarged canines ensured secure prey capture and powerful killing bites, while compressed premolars and elongated metastyles transformed the jaw into a specialised cutting tool. In contrast, modern *P. leo* retains broader, less elongated premolars, reflecting a generalised dentition adapted to savanna conditions and competition for medium-sized ungulates.

Lower dentition (Tables 2, 4). The morphometric analysis of the lower dentition in cave lionesses was based on specimens from Kryshtaleva Cave, Rudky, and Molodova, and Emine-Bair-Khosar. As in the upper jaw, the lower canines show enlargement: their overall length and width are slightly greater, and crown height exceeds mean values of modern lionesses. Lower canines played a crucial biomechanical role in prey capture and killing, penetrating deeply into the neck tissues and forming a locking mechanism with the upper canines. Increased basal robustness prevented fracture under lateral stress during struggles with megafaunal prey, while greater crown height allowed penetration through thick skin and subcutaneous layers. At the same time, cave lion canines are more laterally compressed, proportionally narrower than those of *P. leo*. This morphology reduced resistance during penetration, representing an adaptation to hunting ungulates with thick hides and fat layers (Van Valkenburgh, 1989).

The third lower premolar (p3) in cave lionesses shows reduction and simplification (Marciszak *et al*., 2023): overall length, protoconid length (Lpr), and mesial/distal widths (Ba/Bp) are smaller than mean values of modern lionesses, though still above minimum ranges. This reflects progressive reduction of anterior cheek teeth in favour of the carnassial complex. In generalist predators, p3 retains a broad crown for holding small prey or crushing bones. In *P. spelaea*, p3 became narrower and shorter, losing mechanical significance as functional emphasis shifted posteriorly to the P4/m1 cutting pair (Van Valkenburgh, 1989, 2007).

By contrast, the fourth premolar (p4) remained functionally important. In cave lionesses, protoconid height (Hpr) is lower than in *P. leo*, a trait correlated with increased mechanical strength and resistance to vertical stress. Yet, protoconid length (Lpr) is greater, often approaching maximum values of modern lionesses. This elongation expanded the cutting surface, transforming p4 into a long but low blade optimised for slicing. In some specimens, p4 length approaches that of m1, effectively creating an extended cutting line along the mandible. Such transformation reflects adaptation to efficient meat processing with reduced energetic cost.

The first lower molar (m1) in cave lionesses is longer than mean values of modern African lionesses, though slightly shorter than their maximum. Overall width is marginally greater than *P. leo* averages. This elongation increased occlusal contact between upper and lower carnassials, enhancing efficiency in cutting dense tissues such as ligaments and tendons. However, crown height at the carnassial notch (Hi) is lower than in modern lionesses. In felids, the carnassial notch aids in gripping fibrous food during cutting. A shallower notch in *P. spelaea* indicates a smoother occlusal surface, optimised for slicing soft tissues, whereas *P. leo* retains deeper notches for handling varied prey textures (Van Valkenburgh, 1989, 2007).

Taken together, odontometric analysis of the lower jaw confirms the transition of *P. spelaea* to obligate hypercarnivory. Enlarged lower canines ensured secure capture of megafauna, while reduction of p3 and transformation of p4 into an elongated blade reflect functional optimisation of the carnassial complex. The extended m1 further enhanced cutting efficiency, while reduced crown relief indicates

Table 4. **Lower teeth measurements (mm) of *Panthera spelaea spelaea* from Ukraine compared with extant *Panthera leo.***

Таблиця 4. **Проміри нижніх зубів (у мм) *Panthera spelaea spelaea* з території України у порівнянні з сучасними представниками *Panthera leo.***

Tooth	Locality	*Panthera spelaea spelaea* (Goldfuss, 1810) Kryshtaleva Cave		Kodak	*Panthera leo* Linnaeus, 1758 (extant)					
	Inventory number	OF-806/1964	OF-645/3197	OF-646/3541	6290	5991	6003	5584	1120	6020
	Sex	♀	♂	♂	♂	♂	♀	♀	♀	♀
i1	Total length (L)	–	–	6.1	4.5	–	6.4	–	–	–
	Total width (B)	–	–	4.0	3.6	–	4.8	–	–	–
	Total height (H)	–	–	6.5	6.0	–	6.8	–	–	–
i2	Total length (L)	6.8	–	6.6	5.3	–	7.2	–	–	–
	Total width (B)	5.9	–	5.5	4.5	–	5.9	–	–	–
	Total height (H)	7.9	–	6.6	6.0	–	8.1	–	–	–
i3	Total length (L)	7.2	8.5	7.7	6.3	–	8.8	7.2	–	–
	Total width (B)	7.0	7.7	6.6	5.8	–	7.8	6.3	–	–
	Total height (H)	10.6	8.0	9.5	8.6	–	10.9	8.0	–	–
c1	Total length (L)	16.3	19.8	24.0	16.0	–	21.0	17.8	–	–
	Total width (B)	12.4	14.7	16.5	12.8	–	14.5	13.4	–	–
	Total height (H)	41.6	29.6	45.5	32.0	–	42.0	32.0	–	–
p3	Total length (L)	17.1	19.1	17.5	15.6	–	20.5	17.7	–	19.6
	Protoconid length (L pr)	9.6	9.7	9.2	9.0	–	10.0	9.7	–	–
	Protoconid height (H pr)	10.3	11.0	11.1	9.5	–	10.9	8.4	–	–
	Mesial width (Ba)	6.1	8.5	7.4	7.9	–	9.0	7.3	–	6.5
	Distal breadth (Bp)	8.1	8.0	11.2	8.5	–	11.0	9.9	–	8.6
p4	Total length (L)	25.5	26.9	27.0	23.0	–	28.0	25.9	26.1	25.6
	Protoconid length (L pr)	13.7	11.6	13.0	10.7	–	13.5	11.7	13.1	13.1
	Protoconid height (H pr)	15.2	15.6	18.0	15.6	–	17.7	15.6	17.1	18.3
	Mesial width (Ba)	9.6	11.2	11.5	9.3	–	12.0	11.0	10.5	9.2
	Distal breadth (Bp)	11.4	13.8	14.0	11.7	–	15.6	13.4	13.2	13.6
m1	Total length (L)	26.0	28.6	27.7	18.0	–	30.1	25.7	29.7	29.9
	Paracone length (L pa)	14.5	13.8	13.5	–	–	15.7	13.0	17.0	13.7
	Paracone height (H pa)	15.5	16.5	17.0	–	–	18.3	13.5	15.7	17.5
	Protoconid length (L pr)	16.3	15.6	16.5	–	–	16.0	12.8	16.2	16.3
	Protoconid height (H pr)	14.5	16.6	18.0	–	–	17.7	15.0	16.4	–
	Incisor height (Hi)	9.0	12.3	13.0	–	–	13.0	10.3	10.7	9.7
	Breadth (B)	12.3	14.6	15.0	8.0	–	15.5	14.3	14.0	15.7

specialisation for slicing rather than crushing. Modern *Panthera leo*, in contrast, retains higher crown relief and broader premolars, reflecting a more versatile dentition adapted to diverse prey in the competitive savanna environment.

Comparative craniometric analysis of male cave lions from Ukraine and African lions

Skull and upper jaw (Table 1). The male cave lion sample is represented by a specimen from Chernihiv, compared against two modern male *Panthera leo* skulls. In *P. spelaea*, total skull length and visceral length are smaller than in *P. leo*, whereas condylobasal length and neurocranial length are substantially greater. Biomechanically, this mirrors the trend observed in female mandibles (Table 2): evolutionary shortening of the facial region accompanied by a compressed diastema. Such shortening reduces the distance between canines and the temporomandibular joint, thereby increasing bite force (Sicuro & Oliveira, 2011).

The reduced total length with increased condylobasal length suggests that the occipital crest projected less posteriorly beyond the condyles. This may indicate either a relatively young adult individual or population-specific variation in cervical muscle attachment angles. The enlarged neurocranium points to a more voluminous cranial cavity, consistent with a longer and more massive braincase (Slater & Van Valkenburgh, 2009). The Chernihiv specimen exhibits a wider nasal aperture, a clear marker of climatic adaptation. Cave lions inhabited the cold, arid "mammoth steppe" of the Pleistocene. Expanded nasal openings increased the volume of the nasal cavity, facilitating warming and humidification of inhaled air, thereby protecting the respiratory tract in sub-zero conditions

(Torregrosa *et al*., 2010; Bocherens *et al*., 2011). Despite facial shortening, the specimen shows greater values for maximum canine width, palatal breadth, interorbital foramen width, and pterygoid breadth (Table 1). Rostral expansion provided a robust base for enlarged canines and a wide oral cavity for grasping large prey. The extended postcanine dental row and upper premolar row length reached maximum values of modern lions, reflecting mosaic evolution: a massive dentition integrated into a shortened facial skeleton. Slightly larger interorbital foramina suggest enhanced innervation of vibrissae, supporting heightened tactile sensitivity. Cranial height is also greater, enlarging the temporal fossa and allowing for thicker temporalis musculature, directly increasing bite force capacity (Radinsky, 1989; Meachen-Samuels & Van Valkenburgh, 2009; Sicuro & Oliveira, 2011).

The occipital region demonstrates adaptations like those of the adult Rudky female. Enlarged foramen magnum dimensions imply a thickened spinal cord, while increased width between occipital condyles provided attachment for powerful cervical musculature, essential for subduing megafaunal prey. Expanded auditory bullae indicate acute hearing, advantageous for detecting prey across steppe landscapes. Wide-set orbits, reaching maximum values of modern lions, reflect the species-specific trait of broad binocular vision, facilitating distance assessment in open habitats. Increased minimum postorbital constriction confirms development of massive temporalis muscles, the primary generators of bite force (Radinsky, 1989).

The only width parameters in which the fossil male falls below modern lions are zygomatic and frontal breadth (Table 1). Reduced zygomatic width appears anomalous but may be explained by ontogenetic factors: in male felids, zygomatic arches expand late in development, parallel to masticatory muscle growth. While most measurements of the Chernihiv specimen equal or exceed modern maxima, suggesting a mature adult, zoo-derived *P. leo* specimens often show exaggerated zygomatic breadth due to captivity-related cranial modifications (Cooper *et al*., 2023). Furthermore, the original description (Pidoplichko, 1956) noted damage to one zygomatic arch, reconstructed graphically with dotted lines. This methodological limitation likely introduced error into width calculations, cautioning against overinterpretation.

The Chernihiv male lion confirms species-wide evolutionary trends previously identified in female samples. The skull is characterised by a shortened but broad facial region, a powerful dentition, and an enlarged occipital zone for cervical muscle attachment. This morphology was adapted for securing and overpowering Pleistocene megafauna, generating high bite forces, and functioning efficiently in cold-steppe environments. Expanded nasal apertures reflect physiological adaptation to glacial climates, while reduced zygomatic breadth is best explained by ontogenetic immaturity or reconstruction artefacts rather than true species-level reduction.

Upper dentition (Table 3). The odontometric analysis of the upper dentition in male cave lions is based on the Chernihiv specimen. Measurements demonstrate enlargement of both total length and width of the upper canine (C1), as well as increased length of the second premolar (P2). In males of *P. spelaea*, which hunted Pleistocene megafauna, canines were subjected to extreme bending stresses during killing bites and struggles with prey. Thickening of the canine base provided biomechanical reinforcement, increasing resistance to lateral forces. The enlarged P2 acted as additional structural support for the anterior maxilla, stabilizing the alveoli of massive canines (Van Valkenburgh, 1989, 2007; Bocherens *et al*., 2011).

The third premolar (P3) in the Chernihiv male is longer and broader distally. Whereas female cave lions exhibited lateral compression of P3, the robust male retained or increased its width. Shortened facial morphology generated high bite pressures, requiring broader tooth bases to dissipate stress into the maxilla. Nevertheless, the evolutionary trajectory remained elongation of P3, extending the cutting line of the dental row, while the broadened base provided reinforcement during slicing of dense tissues and tendons (Van Valkenburgh, 2007).

The upper carnassial (P4) shows increased total length and mesial width. Lengthening of P4 reflects hypercarnivory, directly correlated with elongation of the metastyle, the principal cutting blade for muscle fibres. The mesial base of P4 bore the greatest stress during cutting of ligaments and

tendons; its expansion provided stronger anchorage in the maxilla, preventing loosening or fracture under powerful masticatory forces. Thus, the Chernihiv male demonstrates a distinct morphotype: male *P. spelaea* combined elongated cutting edges with thickened basal supports in canines and premolars. This morphology reflects adaptation to extreme bite forces generated by shortened, massive skulls during predation on large Pleistocene prey. Modern male *P. leo*, hunting smaller ungulates, lacks such reinforcement, retaining less massive dental bases.

Lower jaw (Table 2). Analysis of mandibular fragments from Kodak and Kremenchuk reveals shortening of both external and internal dental rows, as well as reduced diastema length compared to modern lions. This metric reduction of the anterior mandible correlates with the previously described shortening of the visceral skull. Functionally, reduced diastema and dental row length brought the canines and carnassials closer to the temporomandibular joint. According to biomechanical principles, decreased distance between force application (teeth) and fulcrum (joint) increases bite pressure. Thus, mandibular shortening in male *P. spelaea* enhanced bite force, consistent with adaptations observed in females (Therrien, 2005).

The most important metric distinction in fossil males is the greater thickness of the mandibular body both anterior to p3 and posterior to m1. Thickening of the bone represents an adaptation to predation on Pleistocene megafauna. When a predator of lion-size subdued massive prey resisting vigorously, the mandible was subjected not only to vertical compressive forces but also to substantial lateral stresses. Biomechanical modelling indicates that increased mandibular thickness is the primary mechanism preventing torsional fracture. The robust mandibles of male *P. spelaea* demonstrate that they regularly encountered active resistance from large prey, whereas modern lions, hunting lighter ungulates, possess thinner jaws. Female *P. spelaea* exhibit more gracile mandibles, suggesting sexual dimorphism in mandibular robustness (Biknevicius & Ruff, 1992; Marciszak & Stefaniak, 2010).

The most ambiguous pattern concerns mandibular height anterior to p3: the Kodak specimen exceeds modern lion values, whereas the Kremenchuk specimen falls significantly below them. Slight reduction is also observed in height posterior to m1 (Table 2). Several hypotheses may explain this variation. Mandibular height in felids is strongly influenced by age and lifetime mechanical loading. The Kodak specimen, with a high, massive mandible, likely represents a fully mature male with extensively developed bone tissue, necessary for attachment of ligaments and muscles. By contrast, the Kremenchuk specimen may belong to a younger individual that had not yet achieved adult bone height. As with the zygomatic arches of the Chernihiv skull, measurements taken from fragmentary remains may carry methodological error: absence of intact basal contours or damage to the bone complicates precise measurement.

Thus, male mandibles of *P. spelaea* from the territory of Ukraine are characterised by evolutionary shortening (reduced diastema and dental row length) combined with mediolateral thickening. This morphology allowed the jaw to generate high bite forces while resisting destructive lateral stresses during struggles with large prey. Intraspecific variability in parameters such as bone height may reflect age-related differences or measurement artefacts.

Lower dentition (Table 4). Analysis of male mandibular dentition, based on specimens from Kodak, Kremenchuk, Volia-Homulecka, and Bilykh Stin Cave, reveals evolutionary restructuring of the third premolar (p3). Crown height (Hpa) and mesial width (Ba) are reduced compared to modern lions, while overall length and protoconid length (Lpr) are increased. As in females, p3 underwent lateral compression and flattening, becoming narrower and longer. Reduction in width and height with simultaneous elongation indicates loss of its crushing function. The tooth was transformed from a tool for breaking hard tissues into an auxiliary blade complementing the posterior carnassial complex (Van Valkenburgh, 1989, 2007, 2008).

The main cutting complex of the male mandible is distinguished by greater length: total m1 length, paraconid length (Lpa) of m1 and protoconid length (Lpr) of p4 and exceed mean values of modern lions. Crown heights (Hpr/Hpa) are also slightly greater. Elongation of proto- and paraconid linearly increased cutting surface area, producing a long blade optimised for slicing soft tissues. As in females, the carnassial notch of m1 is shallower than in *P. leo*.

In modern lions, a deep notch functions as a hook for gripping and severing tendons. Reduction of this feature in *P. spelaea* produced a smoother occlusal surface, transforming m1 into a cutting blade specialised in processing large volumes of muscle fibres from megafaunal carcasses, without bone-crushing capacity.

Particular attention is warranted for the specimen from Bilykh Stin Cave, identified in primary sources as a transitional form (*Panthera spelaea intermedia*? / *Panthera spelaea* ssp.). Its parameters (total length of p4, protoconid dimensions, and m1 width) exceed those of modern *P. leo* and other cave lion specimens analysed but remain smaller than the Sambir tooth attributed to *P. s. fossilis*. This metric profile exemplifies chronocline evolution, i.e. gradual temporal change in species size. *Panthera spelaea intermedia* represents a Middle or early Late Pleistocene stage in cave lion evolution, bridging the large-bodied *P. s. fossilis* and the smaller Late Pleistocene *P. s. spelaea*. The enlarged dimensions and robustness of its dentition confirm the evolutionary trend towards progressive size reduction closer to the end of the glacial period. Dental parameters evolved from the largest in *P. s. fossilis*, through intermediate values in *P. s. intermedia*, to the smallest in Late Pleistocene *P. s. spelaea*. Despite this overall diminution, the dentition of later forms remained highly specialised for hypercarnivory (Marciszak *et al*., 2023).

Odontometric analysis of male mandibles fully corroborates conclusions drawn from female specimens and upper jaws. The dentition of male *P. spelaea* was adapted to hypercarnivory. Interaction between a massive, shortened mandibular bone (capable of generating high bite forces) and elongated, flattened carnassials with shallow notches produced an efficient mechanism for rapid killing of large prey and slicing of soft tissues (Marciszak *et al*., 2023). The transitional specimen from Bilykh Stin Cave further illustrates the evolutionary trend of size reduction during the Late Pleistocene, without loss of functional specialisation. Cave lions retained a deeply adapted dental apparatus, combining biomechanical reinforcement with cutting efficiency, optimised for predation on Pleistocene megafauna.

Acknowledgements

We extend our sincere gratitude to Adrian Marciszak (University of Wrocław, Poland) and Ştefan Vasile (University of Bucharest, Romania) for their constructive comments and thoughtful suggestions.

Declarations

Funding. This research of OK was supported by the National Academy of Sciences of Ukraine (0124U000572).
Conflict of interests. The authors declare that they have no conflicts of interest.

References

Argant, A. (2010). Carnivores (Canidae, Felidae et Ursidae) de Romainla-Roche (Doubs, France). *Revue de Paléobiologie*, *29*(2), 495–601.

Barnett, R., Shapiro, B., Barnes, I., Ho, S. Y., Burger, J., Yamaguchi, N., Higham, T. F., Wheeler, H. T., Rosendahl, W., Sher, A. V., Sotnikova, M., Kuznetsova, T., Baryshnikov, G. F., Martin, L. D., Harington, C. R., Burns, J. A., & Cooper, A. (2009). Phylogeography of lions (*Panthera leo* ssp.) reveals three distinct taxa and a late Pleistocene reduction in genetic diversity. *Molecular Ecology*, *18*(8), 1668–1677. https://doi.org/10.1111/j.1365-294X.2009.04134.x

Barnett, R., Zepeda Mendoza, M. L., Rodrigues Soares, A. E., Ho, S. Y. W., Zazula, G., Yamaguchi, N., Shapiro, B., Kirillova, I. V., Larson, G., Gilbert, M. T. P. (2016). Mitogenomics of the extinct cave lion, *Panthera spelaea* (Goldfuss, 1810), resolve its position within the *Panthera* cats. *Open Quaternary*, *2*, 4. https://doi.org/10.5334/oq.24

Biknevicius, A. R., & Ruff, C. B. (1992). The structure of the mandibular corpus and its relationship to feeding behaviours in extant carnivorans. *Journal of Zoology*, *228*(3), 479–507. https://doi.org/10.1111/j.1469-7998.1992.tb04450.x

Bocherens, H., Drucker, D. G., Bonjean, D., Bridault, A., Conard, N. J., Cupillard, C., Germonpré, M., Höneisen, M., Münzel, S. C., Napierrala, H., Patou-Mathis, M., Stephan, E., Uerpmann, H.-P., & Ziegler, R. (2011). Isotopic evidence for dietary ecology of cave lion (*Panthera spelaea*) in north-western Europe: prey choice, competition and implications for extinction. *Quaternary International*, *245*(2), 249–261. https://doi.org/10.1016/j.quaint.2011.02.023

Cooper, D. M., Yamaguchi, N., Macdonald, D. W., Patterson, B. D., Salkina, G. P., Yudin, V. G., Dugmore, A. J., & Kitchener, A. C. (2023). Getting to the Meat of It: The Effects of a Captive Diet upon the Skull Morphology of the Lion and Tiger. *Animals*, *13*(23), 3616. https://doi.org/10.3390/ani13233616

Diedrich, C. G. (2014a). Holotype skulls, stratigraphy, bone taphonomy and excavation history in the Zoolithen Cave and new theory about Esper's "great deluge". *E&G Quaternary Science Journal*, *63*, 78–98. https://doi.org/10.3285/eg.63.1.05
Diedrich, C. G. (2014b). Palaeopopulations of Late Pleistocene Top Predators in Europe: Ice Age Spotted Hyenas and Steppe Lions in Battle and Competition about Prey. *Paleontology Journal*, *2014*(1), 106203. https://doi.org/10.1155/2014/106203
Ersmark, E., Orlando, L., Sandoval-Castellanos, E., Barnes, I., Barnett, R., Stuart, A., Lister, A., & Dalén, L. (2015). Population demography and genetic diversity in the Pleistocene cave lion. *Open Quaternary*, *1*(4), 1–14. https://doi.org/10.5334/oq.aa
Hemmer, H. (2003). Pleistozäne Katzen Europas: eine Übersicht. *Cranium*, *20*(2), 6–22.
Manuel, M. de, Barnett, R., Sandoval-Velasco, M., Yamaguchi, N., Vieira, F. G., …, & Gilbert, M. T. P. (2020) The evolutionary history of extinct and living lions. *PNAS*, *117*, 10927–10934. https://doi.org/10.1073/pnas.1919423117
Marciszak, A., & Gornig, W. (2024). From giant to dwarf: A trend of decreasing size in *Panthera spelaea* (Goldfuss, 1810) and its likely implications. *Earth History and Biodiversity*, *1*, 100007. https://doi.org/10.1016/j.hisbio.2024.100007
Marciszak, A., & Stefaniak, K. (2010). Two forms of cave lion: Middle Pleistocene *Panthera spelaea fossilis* Reichenau, 1906 and Upper Pleistocene *Panthera spelaea spelaea* Goldfuss, 1810 from the Biśnik Cave, Poland. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, *258*(3), 339–351. https://doi.org/10.1127/0077-7749/2010/0117
Marciszak, A., Ivanoff, D.V., Semenov, Y. A., Talamo, S., Ridush, B., Stupak, A., Yanish, Ye., & Kovalchuk, O. (2023). The Quaternary lions of Ukraine and a trend of decreasing size in *Panthera spelaea*. *Journal of Mammalian Evolution*, *30*, 109–135. https://doi.org/10.1007/s10914-022-09635-3
Marciszak, A., Lipecki, G., Pawłowska, K., Jakubowski, G., Ratajczak-Skrzatek, U., Zarzecka-Szubińska, K., Nadachowski, A. (2020). The Pleistocene lion *Panthera spelaea* (Goldfuss, 1810) from Poland: a review. *Quaternary International*, *605–606*, 213–240. https://doi.org/10.1016/j.quaint.2020.12.018
Marciszak, A., Schouwenburg, C., Gornig, W., Lipecki, G., & Mackiewicz, P. (2019). Morphometric comparison of *Panthera spelaea* (Goldfuss, 1810) from Poland with the lion remains from Eurasia over the last 700 ka. *Quaternary Science Reviews*, *223*, 105950. https://doi.org/10.1016/j.quascirev.2019.105950
Meachen-Samuels, J., & Van Valkenburgh, B. (2009). Craniodental indicators of prey size preference in the Felidae. *Biological Journal of the Linnean Society*, *96*(4), 784–799. https://doi.org/10.1111/j.1095-8312.2008.01169.x
Pidoplichko, I. G. (1956). *Materials for Study of the Past Faunas of the UkrSSR*, is. 2. Vydavnytstvo Akademii Nauk Ukrainskoi RSR, Kyiv. [Ukrainian]
Radinsky, L. B. (1981). Evolution of skull shape in carnivores: 1. Representative modern carnivores. *Biological Journal of the Linnean Society*, *15*(4), 369–388. https://doi.org/10.1111/j.1095-8312.1981.tb00770.x
Schmid, E. (1940). Variationsstatistische Untersuchungen am Gebiß pleistozäner und rezenter Leoparden und anderer Feliden. *Zeitschrift für Säugetierkunde*, *15*, 1–179.
Segura, V., Cassini, G. H., & Prevosti, F. J. (2016). Three-dimensional cranial ontogeny in pantherines (*Panthera leo*, *P. onca*, *P. pardus*, *P. tigris*; Carnivora, Felidae). *Biological Journal of the Linnean Society*, *120*(1), 210–227. https://doi.org/10.1111/bij.12888
Sicuro, F. L., & Oliveira, L. F. B. (2011). Skull morphology and functionality of extant Felidae (Mammalia: Carnivora): a phylogenetic and evolutionary perspective. *Zoological Journal of the Linnean Society*, *161*(2), 414–462. https://doi.org/10.1111/j.1096-3642.2010.00636.x
Slater, G. J., & Van Valkenburgh, B. (2009). Allometry and performance: the evolution of skull form and function in felids. *Journal of Evolutionary Biology*, *22*(11), 2278–2287. https://doi.org/10.1111/j.1420-9101.2009.01845.x
Sotnikova, M., & Nikolskiy, P. (2006). Systematic position of the cave lion *Panthera spelaea* (Goldfuss) based on cranial and dental characters. *Quaternary International*, *142–143*, 218–228. https://doi.org/10.1016/j.quaint.2005.03.019
Therrien, F. (2005). Mandibular force profiles of extant carnivorans and implications for the feeding behaviour of extinct predators. *Journal of Zoology*, *267*(3), 249–270. https://doi.org/10.1017/S0952836905007430
Torregrosa, V., Petrucci, M., Pérez-Claros, J. A., & Palmqvist, P. (2010). Nasal aperture area and body mass in felids: Ecophysiological implications and paleobiological inferences. *Geobios*, *43*(6), 653–661. https://doi.org/10.1016/j.geobios.2010.05.001
Van Valkenburgh, B. (1989). Carnivore Dental Adaptations and Diet: A Study of Trophic Diversity within Guilds. In: *Carnivore Behavior, Ecology, and Evolution*. https://doi.org/10.1007/978-1-4613-0855-3_16
Van Valkenburgh, B. (2007). Deja vu: the evolution of feeding morphologies in the Carnivora. *Integrative and Comparative Biology*, *47*(1), 147–163. https://doi.org/10.1093/icb/icm016
Van Valkenburgh, B. (2008). Costs of carnivory: tooth fracture in Pleistocene and Recent carnivorans. *Biological Journal of the Linnean Society*, *96*(1), 68–81. https://doi.org/10.1111/j.1095-8312.2008.01108.x
White, H. E., Camaiti, M., Tucker, A. S., Watanabe, A., & Goswami, A. (2026). A suture in time: The ontogeny of cranial suture morphology in mammals. *Journal of Anatomy*, *248*(3), 501–516. https://doi.org/10.1111/joa.70035