

Bulletin of the Natural History Museum, 2025, 18: 29-44.

Received 16 Jun 2025; Accepted 01 Sep 2025.

doi:10.5937/bnhmb2518029A

UDC: 56:599.742.734(497.11)"628.62"

Original scientific paper

REMAINS OF THE EURASIAN LYNX (*LYNX LYNX*, CARNIVORA, MAMMALIA) FROM MANDINA CAVE (EASTERN SERBIA)

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This study provides a description of the ancient cranium and both branches of the mandible of a male Eurasian lynx (*Lynx lynx*) from Mandina Cave (Eastern Serbia). Cranial, mandibular, and dental measurements were obtained using standard methodology, and their analysis allowed comparisons with other known remains of the Eurasian lynx, as well as with the geographically closest extinct and recent subspecies.

Key words: *Lynx lynx*, Mandina Cave, cranium, mandible

INTRODUCTION

Mandina Cave is located five kilometers north of the village of Zlot, Bor municipality, on the right side of the Beljevina River Gorge, at the foot

of the Stobori Hill and Dubašnica karst surface, at an altitude of 370 meters. Until 1976, it was completely unknown and inaccessible, even to the local population. Paleontological and biological research began only in the early 1990s. Material was collected on several occasions.

By sieving sediment from the surface layer at several points within the cave, numerous vertebrate remains were recovered. Among them, the most common are fossil and subfossil osteological and dental material of small and large mammals. Paleontological analysis determined the presence of the following species: *Talpa europaea*, *Erinaceus roumanicus*, *Sorex araneus*, *Crocidura leucodon*, *Rhinolophus ferrumequinum*, *Rhinolophus euryale*, *Myotis bechsteinii*, *Ochotona pusilla*, *Lepus europaeus*, *Spermophilus citellus*, *Sciurus vulgaris*, *Glis glis*, *Mus musculus*, *Apodemus sylvaticus*, *Rattus rattus*, *Sicista subtilis*, *Cricetus cricetus*, *Nothocricetulus migratorius*, *Mesocricetus newtoni*, *Lagurus lagurus*, *Arvicola terrestris*, *Chionomys nivalis*, *Myodes glareolus*, *Microtus arvalis*, *Microtus (Terricola) subterraneus*, *Spalax leucodon*, *Canis lupus*, *Vulpes vulpes*, *Ursus* sp., *Mustela putorius*, *Meles meles*, *Martes foina*, *Lynx lynx*, *Capreolus capreolus*, *Cervus elaphus*, and *Ovis ammon* (Paunović & Marković 1994, Marković 1998). Among these finds is a very well-preserved lynx cranium with both branches of the mandible. The cranium was discovered in 1993, 50 meters from the entrance on the cave floor, by two then-young researchers (Ivo Karaman and Slobodan Marković), participants in a geological-biological research campaign in the Bor region. The find was handed over to members of the team from the Natural History Museum in Belgrade (NHMBEO). During a subsequent entry of NHMBEO paleontologists and biologist into the cave, the mandible was discovered in close proximity to the site of the first find. Both the cranium and mandible were covered by a thin layer of clay and silt, which was carefully removed by museum preparators, allowing all features to be observed and necessary measurements to be taken.

MATERIAL AND METHODS

Cranium of the male Eurasian lynx [*Lynx lynx* (Linnaeus, 1758)] with both branches of the mandible. The material is housed in the Quaternary Large Mammals Collection of the Natural History Museum in Belgrade, under inventory numbers Q LM MAN 215, Q LM MAN 216, Q LM MAN 217. It is in good condition, with the major part of the cranial and mandibular structure preserved. The absolute age of the remains, determined by radiocarbon (C14) dating, taken from the right mandibular fragment is 11,681 cal yr BP. Dating was conducted at the ETH Augmented Reality Research Laboratory in Zurich, Switzerland.

The study includes 10 cranial measurements (Tab. 1), four mandibular angles (Tab. 2) and specific lengths of the teeth and mandible were recorded (Tables 3–5). All measurements were taken using a digital caliper with an accuracy of 0.1 mm. For the measurement and definition of mandibular angles, the literature was followed (Onar *et al.* 1997), while cranial indices were calculated according to the methodology described by Onar (1999) (Fig. 1). Morphological terminology for describing and

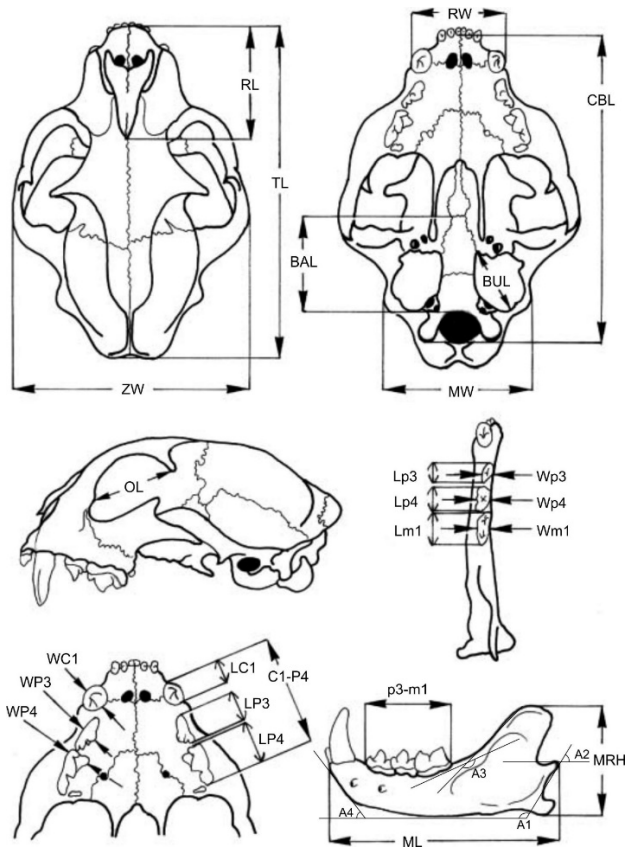


Fig. 1. – Description of the traits measured. Thirteen traits are related to the cranium or mandible: TL, total length of cranium; CBL, condylobasal length of cranium; BAL, basicranial axis length; RL, rostral length; OL, orbital length; ZW, zygomatic width; MW, mastoid width; RW, rostral width; BUL, bullar length; ML, mandible length; MRH, mandible ramus height; C1–P4, C1 to P4 length; p3–m1, p3 to m1 length.

identifying skull and dental structures follows Gomerčić (2005), Ghezzi *et al.* (2014), and Dayan *et al.* (2017). Dental measurements included the length of the alveolar rows (C1–P4 in the upper jaw and p3–m1 in the lower), crown width and height, and the height of the mandibular corpus in

front of p3, allowing an assessment of the proportional development of the tooth row and its adaptation to the type of diet. The tables present the results of the obtained cranial, mandibular, and angular measurements. Tab. 1 contains basic cranial dimensions, relating to length, width, and proportions between the rostral and cranial parts, providing insight into overall cranial proportions. Tab. 4 includes key mandibular measurements, including tooth row length and ramus height, enabling comparisons of the morphological proportions of the lower jaw. Tab. 2 presents measurements of the four mandibular angles, important for understanding morphological differences in the jaw structure and its adaptation to chewing function. Tables 3 and 5 provide dimensions of the teeth of the upper and lower jaws.

PALEONTOLOGICAL SECTION

Systematic paleontology

Class: Mammalia Linnaeus, 1758

Order: Carnivora Bowdich, 1821

Family: Felidae Fischer de Waldheim, 1817

Subfamily: Felinae Fischer de Waldheim, 1817

Genus: *Lynx* Kerr, 1792

Lynx lynx (Linnaeus, 1758)

Material and Measurements

Cranium (Inv. no. Q LM MAN 215),

(Tab. 1; Tab. 2; Fig. 1: a-f)

Left branch of lower jaw with preserved c1-m1 (Inv. no. Q LM MAN216),

(Tab. 2; Tab. 4; Fig. 2: a-c)

Part of the right branch of the lower jaw with preserved p3-m1 (Inv. no. Q LM MAN217),

(Tab. 3; Fig. 2: d-f)

Cranium. Very well-preserved, elongated oval in shape with rather prominent zygomatic arches. Laterally, a high frontal bone profile is observed. The parietal bone slopes almost vertically toward the occipital region. On the dorsal side, a prominent sagittal suture and a long, sharp sagittal crest extending into a wide occipital bone provide mandibular strength. Foramen magnum is oval, slightly wider at its base. Auditory

bullae are well-preserved, ellipsoid in shape, composed of a single chamber. The jugular and hypoglossal foramina are clearly separated.

Table 1. – Cranium measurements (mm).

TL	Total length	158.0
RL	Rostral length	78.7
ZW	Zygomatic width	119.5
OL	Orbital length	38.8
CBL	Condylbasal length	153.2
BAL	Basicranial axis	50.6
C1-P4	C1 to P4 length	51.5
BUL	Bullar length	25.4
MW	Greatest mastoid breadth	68.9

Table 2. – Angle measurements taken from the mandible (mm).

A1	Angle between margo ventralis mandibulae and margo caudalis mandibulae	94°
A2	Angle between tuber mandibulae of the condylar process and margo caudalis mandibulae	86°
A3	Angle between ramus mandibulae and margo alveolaris of pars molars corporis mandibulae	160°
A4	Angle between rostral edge of the corpus mandibulae and the margo ventralis mandibulae	50°

The first and second incisors, I1 and I2, are present in the left half of the upper jaw, while only I2 is preserved in the right. The left upper canine C1 is robust, with an ellipsoid cross-section. Two parallel sutures are visible on the buccal side of the canine. The right canine is broken at the base, only the root is preserved in the jaw. Based on the morphology of the fracture and the opening above it on the maxillary bone, it is evident that the animal lost it before death and used the broken canine as a premolar, with the root penetrating the right maxillary bone. The upper third premolar P3 is characterized by a high, circular paracon. The metastyle is well-developed, circular with a pronounced distal cingulum. The upper fourth premolar P4 is characterized by a small diagonally oriented protocone. The parastyle is well-developed and of the same height as the metastyle; the ectoparastyle is also developed. The paracon is well-developed, sharp, and mesiodistally prominent relative to the metastyle.

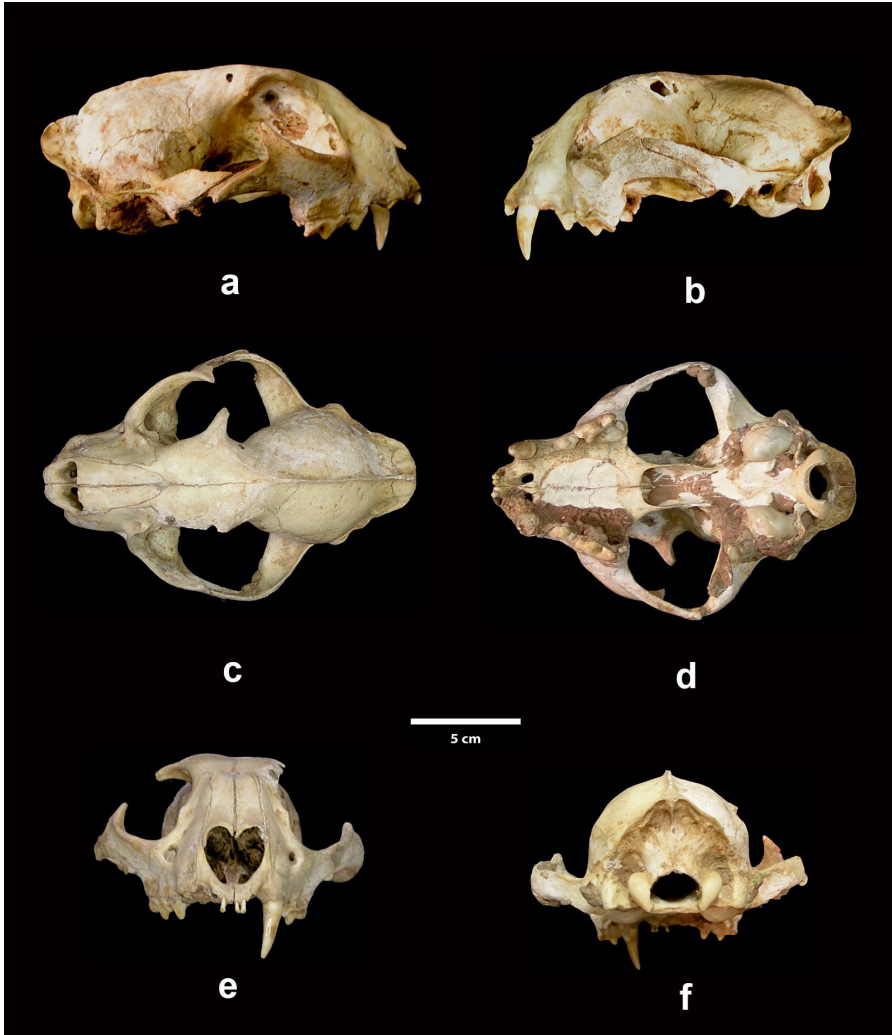


Fig. 2. – Cranium (Inv. no. Q LM MAN 215): a) right lateral view; b) left lateral view; c) dorsal view; d) ventral view; e) anterior view; f) posterior view.

Table 3. – Measurements (in mm) of the upper dentition: L – mesiodistal length, W – labiolingual breadth, Lproto – mesiodistal length of P4 protocone, Lpara – mesiodistal length of P4 paracone, Lmeta – mesiodistal length of P4 metastyle.

Upper dentition	C1		P3		P4				
	L	W	L	W	L	W	Lproto	Lpara	Lmeta
Left	9.2	7.7	11.3	6.4	20.2	7.6	3.5	6.8	7.6
Right	missing		11.2	6.2	20.5	7.5	3.4	6.7	7.3

Mandible. The left mandible branch is well-preserved, robust, with c1, p3-m1, and alveoli for i1-i3. The coronoid process is broken. The jaw is almost straight, giving the lynx a pronounced chin, with a short diastema and two mental foramina. The masseteric fossa is deep, reaching the level of the distal root of the first molar. The right mandible branch with p3-m1 and alveolus of c1 is broken at the level of the distal root of m1. The canine is strong and sharp, with two sutures present on the buccal-lateral side. The third lower premolar p3 is almost symmetrical, buccolingually compressed, with a high protoconid and moderately developed paraconid. Buccally, especially in the right third premolar, a developed distal cingulid is observed. The protoconid on p4 is symmetrical laterally, with an incipient distal cingulum. In m1, the protoconid is higher than the paraconid, while the mesiodistal length is equal; the metaconid is present (Fig. 5 d).

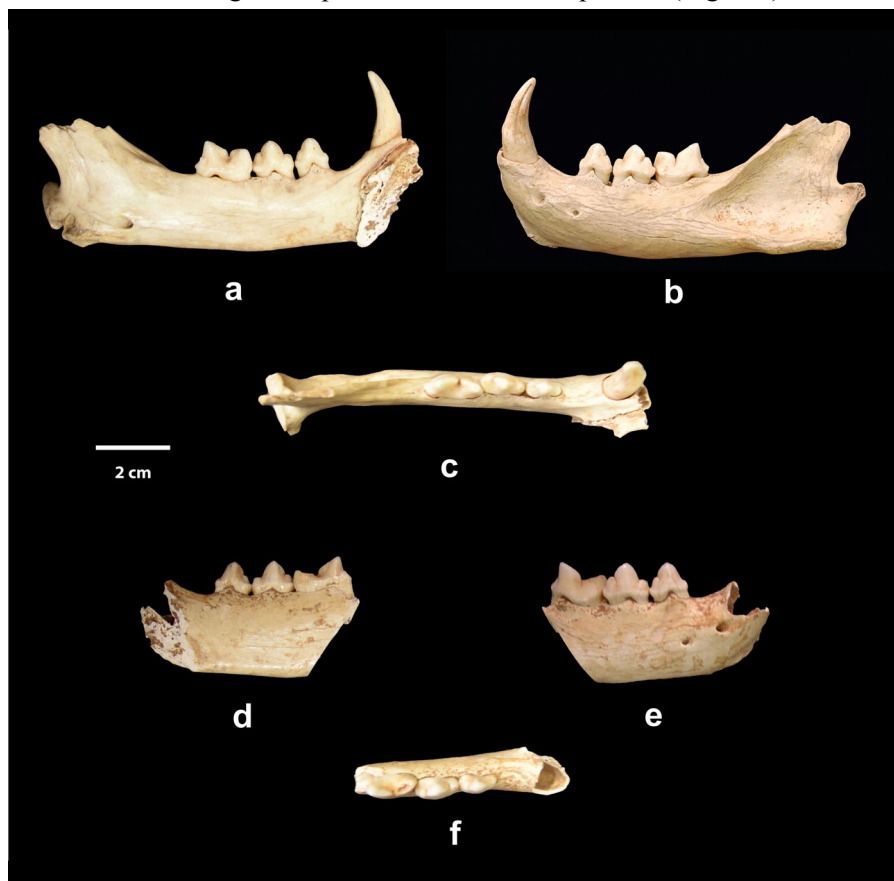


Fig. 3. – Mandible: a) left branch of the lower jaw with preserved c1-m1 (Inv. no. Q LM MAN216) Left hemimandible with c1-m1, lingual view; b) buccal view; c) occlusal view; d) part of right hemimandible with p3-m1 (Inv. no. Q LM MAN217), lingual view; e) buccal view; f) occlusal view.

Table 4. – Mandible measurements (mm).

ML	Mandible length	106.7
p3-m1	Length of the cheektooth row	37.3
MRH	Mandible ramus height	~44.0
MH	Height of the mandible in front of p3	21.4

Table 5. – Measurements (in mm) of lower dentition: L – mesiodistal length, W – labiolingual breadth, Lprotid – mesiodistal length of m1 protoconid, Lpard – mesiodistal length of m1 paraconid.

Lower dentition	c1		p3		p4		m1			
	L	W	L	W	L	W	L	W	Lprotid	Lpard
Left	8.5	7.4	9.3	5.1	12.3	6.3	15.5	6.8	7.3	6.3
Right	missing		9.7	5.1	12.1	6.2	15.7	6.7	7.0	6.9

DISCUSSION

Measurement results indicate that the Mandina Cave lynx cranium belongs to a large, adult male, whose dimensions are at the upper range of variability for the species. Such values may result from a combination of ontogenetic and ecological factors, as cranial dimensions in the Eurasian lynx differ significantly between sexes, age classes, and geographic populations. Recorded values also confirm the tendency toward increased size in populations from mountainous and colder regions, in accordance with Bergmann's rule (Breitenmoser *et al.* 2000).

Comparing basic craniometric characteristics (Tab. 6) of the Mandina Cave male with the mean values of recent Eurasian lynx populations shows significant deviations in maximum and condylobasal length, as well as in zygomatic and mastoid width. Maximum and condylobasal lengths exceed the largest measured cranial lengths of a 15-year-old male lynx from Croatia (Gomerčić 2005). It can also be noted (Tab. 6) that the Mandina Cave lynx cranium dimensions are larger compared to the subspecies *L. lynx balcanicus* and *L. lynx dinniki*, while fitting within the range of the Carpathian lynx (*L. lynx carpathicus*) (Kratochvíl 1981, Werdelin 1981, Hemmer 1993). The Carpathian subspecies (*L. lynx carpathicus* Kratochvíl & Štollman 1963), described based on specimens from the Slovak Carpathians (Malá Fatra), represents the largest European subspecies,

surpassed in size only by subspecies from Central and Eastern Asia (Mirić 1981). Carpathian specimens are on average larger than *L. lynx dinniki*. The significant width of zygomatic arches in the Carpathian subspecies stands out, showing higher values compared to nominal form specimens (Mirić 1981). Indices include cranial index (47.58), skull index (70.57), and facial index (174.2), allowing comparison of proportional relationships between cranial length and width, as well as between cranial and facial parts. The specific pentagonal shape of the presphenoid bone observed in our specimen is characteristic of *L. lynx* (Tura-Poch *et al.* 2022) (Fig. 4 c).

Table 6. – Comparative morphometric data of male lynx subspecies cranium (mm).

Morphom. values	<i>L. lynx</i> (Mandina cave)	<i>L. lynx carpathicus</i> (Croatia) (Gomerčić <i>et al.</i> 2010)	<i>L. lynx balcanicus</i> (Serbia) (Mirić 1981)	<i>L. lynx carpathicus</i> (Czech) (Štollman 1963)	<i>L. lynx dinniki</i> (Caucasus region) (Štollman 1963)
TL	158.0	153.2	151.8	158.2	153.0
CBL	153.2	142.8	136.5	141.3	135.7
ZW	119.5	111.3	106.1	109.9	107.5

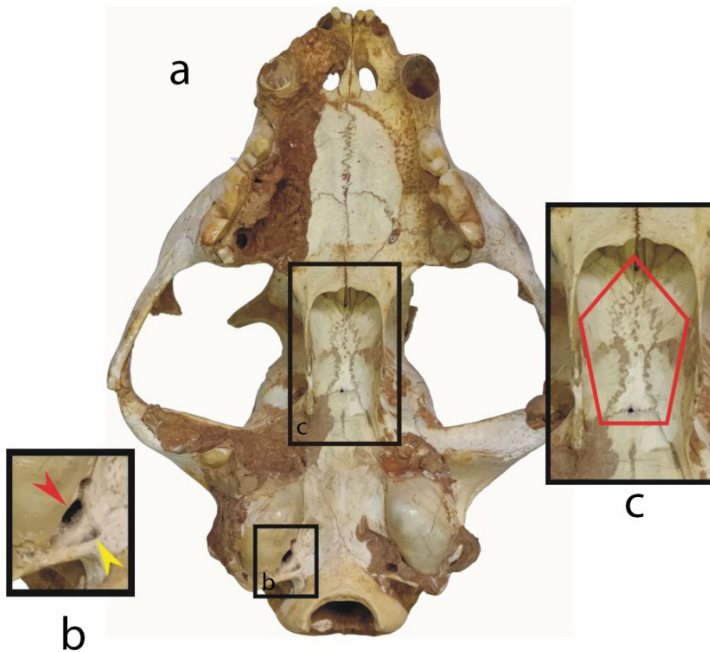


Fig. 4. – a) dorsal view of the cranium; b) jugular and hypoglossal foramina. Red arrow indicate the posterior lacerate (or jugular) foramen; yellow arrow indicates the hypoglossal (or anterior condyloid) foramen; c) presphenoid bone.

In felids, skull and mandible shape influence bite force and prey-capture ability (Slater & Van Valkenburgh 2009, Christiansen 2008, Figueirido *et al.* 2013). Accordingly, measured cranial indices and mandibular angles in the ancient Mandina Cave lynx suggest adaptations for handling larger prey.

Besides ontogenetic factors, cranial morphology may reflect ecological and trophic adaptation. Greater cranial robustness in the lynx may be associated with feeding habits and seasonal prey availability, as cranial features in carnivores often reflect adaptation to their trophic niche (Figueirido *et al.* 2011, Nowak 1999, Breitenmoser *et al.* 2000). Changes in living conditions may, according to some authors, lead to relatively rapid morphological changes within a population (Pertoldi *et al.* 2005, Gál *et al.* 2022).

Certain cranial traits can provide important data on ontogenetic changes and taxonomic affiliation. For example, the prominence of the sagittal crest and other cranial structures changes during growth, reflecting changes in the size and strength of the musculature in felids (Stefen & Heidecke 2012). In the Mandina Cave specimen, the strongly developed sagittal crest along the parietal part of the cranium may indicate well-developed temporal muscles, often characteristic of adult males after cranial growth completion. Paleo-osteological analyses of lynx show relatively conservative cranial morphology patterns in the late Pleistocene and early Holocene, suggesting that basic cranial dimensions and tooth proportions remained stable within the species over long time intervals (Boscaini *et al.* 2016, Gál *et al.* 2022). Carnivore skull shape is linked to bite force and prey type, as cranial structures are adapted to the stresses occurring during prey capture and processing (Van Valkenburgh 2007).

Separation of the jugular and hypoglossal foramina is considered one of the most important traits distinguishing *Lynx lynx* from *Lynx pardinus*, in which the two foramina are in the same cavity (Boscaini *et al.* 2016, Mecozzi *et al.* 2021). Examination of this feature in recent and ancient Asian species showed that the joining of the posterior jugular and hypoglossal foramina is present in most species – *Lynx rufus*, *Lynx pardinus*, and *Lynx hei*. However, in *Lynx canadensis* and *Lynx lynx*, the two foramina are clearly separated. Most *Lynx issiodorensis* specimens show the presence of two foramina in the same cavity, considered a primitive condition for cats, including the genus *Lynx*. In our cranium, the foramina separation is noticeable (Fig. 4 b).

Premolars of the ancient Mandina Cave lynx show the presence of pronounced longitudinal grooves along the buccal and lingual surfaces (Fig. 5a–b). Similar to *Lynx issiodorensis*, early Pleistocene representatives

of the genus *Lynx* also have pronounced longitudinal grooves on premolars (Jianzuo *et al.* 2022, Lavrov *et al.* 2021). The ectoparastyle is usually present on P4 in *L. lynx* (Mecozzi *et al.* 2021, Kurtén 1978), which was also observed in our specimen (Fig. 5c). These morphological features are important diagnostic elements for taxonomic identification of ancient lynxes and allow comparison of their morphological characteristics with other Pleistocene representatives of the genus *Lynx*, with tooth dimensions indicating that our specimen did not differ significantly from currently known Eurasian populations (Kratochvíl 1981, Hemmer 1993).

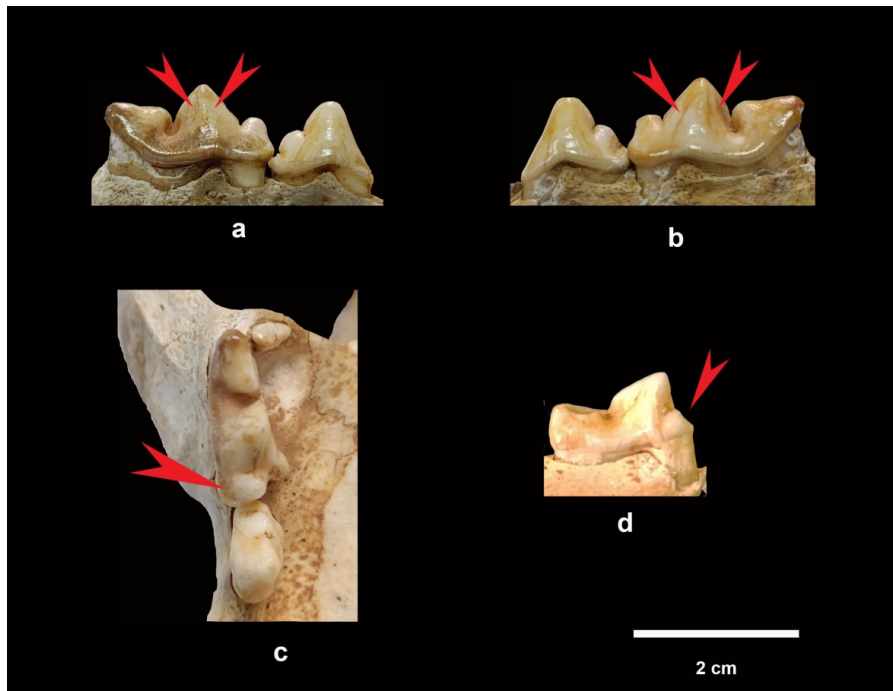


Fig. 5. – Details of P4 and m1: a–b) Vertical buccal grooves on P4; c) ectoparastyle on P4; d) metaconide on carnassial m1.

CONCLUSION

The cranium of the Mandina Cave male lynx, based on its morphometric characteristics, shows clear deviations compared to most of the compared recent Eurasian lynx populations. Cranial dimensions, especially maximum and condylobasal lengths, as well as the width of zygomatic arches and mastoid width, indicate that the specimen cannot be assigned to the Balkan or Oriental subspecies, whose values are signi-

ificantly smaller. At the same time, the dimensions correspond to the range of the Carpathian subspecies (*Lynx lynx carpathicus*), known for its large size and broad zygomatic arches. Furthermore, the presented cranial, mandibular, and dental dimensions, the determined absolute age of the remains, the geographic location of Mandina Cave as their site, and the established relationships among mitogenome haplotypes of different recent populations relative to the timeline of their divergences (Lucena-Perez *et al.* 2019), provide grounds for considering that the specimen belongs to the Carpathian population lineage. However, caution is needed when drawing conclusions, as exceptions are possible – such as the case of four male lynxes from Turkey, whose craniometric parameters and skull shape are closer to the Iberian lynx than to the introduced specimens of the Carpathian population from Croatia (Dayan *et al.* 2017).

Based on dating results, the absolute age of the remains is established at 11,681 yrs BP. This means that this lynx individual lived precisely at the transition between the Pleistocene and Holocene (MIS 2; Last Glacial). Consequently, the entire mammal assemblage from Mandina Cave can be characterized as transitional fauna, simultaneously containing cold, steppe, ubiquitous, and thermophilic species. Species characteristic of cold steppes, still inhabiting such areas today, include *Ochotona pusilla*, *Nothocricetulus migratorius*, and *Lagurus lagurus*. All other representatives can be characterized as “modern” species inhabiting the Balkan Peninsula. The only extinct species is ancient *Ursus* sp.

Although this study has significant limitations, as comparisons were made only based on morphometric data of a single cranium, we believe it will contribute to future research, given that a complete description and metric data for the cranium and teeth of the male Eurasian lynx are provided. Additional studies, including DNA analyses, could confirm the taxonomic status of the specimen and more precisely define the relationship between Balkan and Carpathian populations. Moreover, comparisons with archeozoological finds from the Dinarides, Carpathians, Balkanides and Pannonian Basin region could contribute to understanding postglacial species migrations.

Acknowledgments. We thank Miloš Milivojević, Senior Geological Preparer at NHMBEO, for preparing the material for paleontological processing and photography. We also express our gratitude to Dr. Emilia Hofman-Kamińska and Dr. Rafał Kowalczyk from the Mammal Research Institute, Polish Academy of Sciences, for data on the absolute age of the remains.

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ОСТАЦИ ЕВРОАЗИЈСКОГ РИСА (*LYNX LYNX*, CARNIVORA, MAMMALIA) ИЗ МАНДИНЕ ПЕЋИНЕ (ИСТОЧНА СРБИЈА)

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РЕЗИМЕ

Анализирани фосилни остаци евроазијског риса (*Lynx lynx*) потичу из Мандине пећине, која се налази пет километара од села Злот, у општини Бор, источна Србија. Материјал обухвата добро очуван кранијум и леву и десну грану мандибуле, откривене током истраживања 1993. године. Радиокарбонском анализом утврђена је старост од 11 681 калибрисаних година пре садашњости, што овај налаз смешта у завршну фазу плеистоцена, почетак холоцена. Морфометријска анализа обухватила је мерења лобање, вилице, зуба и мандибуларних углова, чиме су дефинисане пропорције и карактеристике скелета.

Резултати показују да примерак припада крупном одраслом мужјаку, са димензијама које прелазе просечне вредности савремених популација. Посебно се издвајају веће вредности укупне дужине лобање, кондилобазалне дужине и ширине зигоматичних лукова. Јасно раздвојени југуларни и хипоглосни отвор потврђују припадност врсти *Lynx lynx*, док упоредна анализа указује да ове карактеристике одговарају карпатској подврсти (*Lynx lynx carpathicus*). Морфолошке особине, укључујући изражен сагитални гребен и робустну мандибулу, указују на снажно развијену мускулатуру и адаптацију на исхрану крупнијим пленом. Пратећа фауна указује на мешавину степских и савремених врста, што одражава климатске промене на крају плеистоцена.“

Иако се закључци заснивају на једном примерку, резултати указују на повезаност овог налаза са карпатском популационом линијом риса. Даља истраживања, нарочито анализе ДНК, неопходна су за прецизније разјашњење таксономског статуса и постглацијалних миграција ове врсте.