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EVOLUTIONARY TRENDS IN THE FOURTH LOWER PREMOLAR OF *URSUS ROSSICUS* BORISSIAK, 1930: MOLARISATION OF P4 IN SPELAEOID BEARS

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Abstract: A detailed study was conducted of the fourth lower premolar (p4) of *Ursus rossicus* from several localities, representing different temporal stages in the evolution of the Eurasian Pleistocene biota. Distinctive features were identified of p4 molarisation at various stages of the evolution of small cave bears. The lower fourth premolar *U. rossicus nordostensis* from the Pleistocene of Arctic Siberia shares with *U. rossicus* s. l. the derived morphology of the lingual trigonid cusps, but retains the basal deningeroid trait, such as the narrowed distal contour of the crown of p4. By the end of the Middle Pleistocene, p4 of *U. rossicus* exhibited a maximum molarisation, displaying a multicuspidate pattern in both the trigonid and talonid parts, as observed in the type series from the Krasnodar locality and additional material from the Irgiz 1 locality. At the same time, the Late Pleistocene set of p4 from the Imanay locality, while having most of the *U. rossicus* characteristics, displayed a wide spectrum of morphotypes, ranging from simple to a multicuspidate one. Additionally, it was revealed that molarisation of p4 in cave bears followed a different evolutionary trajectory. In *U. rossicus*, there was a complication on both trigonid and talonid. In contrast, in large cave bears, mostly the trigonid part of p4 became complicated, while the talonid remained relatively short, lacking most additional cusps.

Key words: *Ursus rossicus*, *Ursus kanivetz*, cave bear, Pleistocene, dental variability, morphology, fourth premolar

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Introduction

During the last 20 years, since the last major review of the family Ursidae (Baryshnikov 2007), opinions on the taxonomy of spelaeoid bears have evolved. Currently, these ursids are divided into four groups: deningeroid bears, Caucasian cave bears, large cave bears, and small cave bears. The first group comprises two species: *Ursus deningeri* von Reichenau, 1904 and *Ursus deningeroides* Mottl, 1964. The Caucasian cave bear group includes *U. praekudarensis* (Baryshnikov, 1998) and *U. kudarensis* Baryshnikov, 1985. The group of large cave bears includes *Ursus spelaeus* Rosenmüller, 1794 with numerous subspecies.

Among the small cave bears, the most notable is the Russian cave bear, *Ursus rossicus* Borissiak, 1930. The species *Ursus savini* Andrews, 1922, which was previously attributed to this group, was discussed and considered invalid in some studies. For example, Rabeder et al. (2010) suggested that *U. savini* represents a junior synonym of *U. deningeri*. More cautious conclusions were presented by Baryshnikov and Puzachenko (2020), based on a comprehensive mathematical analysis of dental characteristics. These authors characterized *U. savini* as "a controversial taxon" having "a unique combination of characters" within an evolutionary line of spelaeoid bears.

The modern phylogenetic model of spelaeoid bears integrates morphological and molecular data (Baryshnikov 2007, Knapp et al. 2009, Baryshnikov and Puzachenko 2011, 2017, 2019, 2020, Stiller et al. 2014, Barlow et al. 2018, 2020, 2021). Nuclear genome analyses confirmed the independence of a separate Caucasian clade (*praekudarensis* and *kudarensis* lineage), which forms a sister group to other cave bears (Barlow et al. 2021). Molecular evidence further suggested a substantial phylogenetic distance between the small cave bear *U. rossicus* and the European large cave

bear clade (Barlow et al. 2021), confirming *U. rossicus* as a phylogenetically isolated and highly divergent species.

As for the distribution of spelaeoid bears in Russia, their most ancient representatives have rarely been found there. Indeed, the Early and Middle Pleistocene records of *U. deningeri* are numerous in Western Europe, but in Russia, this taxon is poorly known (Baryshnikov 2007). Other spelaeoid forms, *U. spelaeus* s. l. and *U. kanivetz*, were widespread in the Late Pleistocene in Europe, where the latter taxon was known as *U. k. ingressus* Rabeder et al., 2004. Its eastern counterpart, *U. k. kanivetz*, occurred in the Urals (Baryshnikov 2007, Gimranov and Kosintsev 2022). In the Caucasus, *U. praekudarensis* and *U. kudarensis* existed during the Middle and Late Pleistocene (Baryshnikov 2020, Duno-Iglesias et al. 2024). *U. rossicus* was occasionally found in southern Europe's Middle and/or Late Pleistocene, but most of the records come from southern Russia, the pre-Ural region, and Siberia, with only sparse additional records from northern Asia (Baryshnikov 2007, Sher et al. 2011, Boeskorov and Baryshnikov 2013).

Due to the wide distribution and abundant records of large cave bears, substantial data are available on their morphology, feeding behaviour, ecology, chronology, and evolution (Torres 1984, Baryshnikov 2007, Pacher and Stuart 2009, Baca et al. 2016, Van Heteren and Figueirido 2019, Veitschegger et al. 2019, Bocherens 2019, Charters et al. 2019, Pappa et al. 2019, Pérez-Ramos et al. 2019, 2020, Naito et al. 2020, Galdies 2022, Gimranov and Kosintsev 2022, Ramírez-Pedraza et al. 2022). In contrast, information about *U. rossicus* remains scarce, with its origins, dispersal, and evolutionary trends still not fully understood. Its phylogenetic relationships with other spelaeoid bears also remain a subject of debate.

The morphology of cheek teeth in spelaeoid and arctoid bears was extensively studied (e.g., Rode 1935, Rabeder 1983, 1989, 1999, Baryshnikov 2007, 2020, Gimranov 2018). Evolutionary changes in the structure of the fourth lower premolar (p4) were traced for *U. deningeri* (Rabeder 1999, Baryshnikov 2007, Marciszak et al. 2025), *U. spelaeus* s. l. (Rabeder 1983, 1989), and *U. kudarensis* (Baryshnikov 2020). Similarly, the morphology of p4 was studied in both extant and fossil brown bears, *Ursus arctos* Linnaeus, 1758 (Torres 1984, Gimranov 2018). However, detailed descriptions of *U. rossicus* p4 are limited to the works of Borissiak (1930, 1932), Vereschagin and Baryshnikov (2000), Baryshnikov and Foronova (2001), Baryshnikov (2007) and Spassov et al. (2017). Therefore, any new insights into its dental morphology are of significant interest.

One of the important characteristics of the spelaeoid bears is their advanced molarisation of p4, accompanied by the buccolingual expansion of its crown and the development of a multicuspidate occlusal surface. This feature is so important in the taxonomy of spelaeoid bears that Baryshnikov (2007) incorporated p4 traits into species diagnoses. However, the high plasticity of p4 morphology makes it necessary to understand the range of its variation. *U. rossicus* exhibits the highest degree of p4 molarisation among spelaeoid bears, making it a subject of particular interest for evolutionary and morphological research.

Material and methods

The current study of the fourth lower premolar of *U. rossicus* is based on the new material, which includes a substantial collection from the Imanay Cave (Southern Urals) and material from the Irgiz 1 locality (Volga River basin). Additionally, the type collection of *U. rossicus*, and the holotype of *Ursus rossicus nordostensis* Baryshnikov, 2011 were re-examined. This material provides data on the evolutionary trends of p4 in small cave bears throughout almost the entire existence of *U. rossicus*, specifically, from the end of the Early to the end of the Late Pleistocene.

The oldest and most primitive p4 of *U. rossicus* was found in the left hemimandible (IAM No. F-2365) of *U. r. nordostensis*, discovered above the Arctic Circle at the Ovrag locality near Cherskiy (Kolyma River basin, Arctic Russia, 68° 73′ N, 161° 38′ E; Text-fig. 1). Originally described as *U. savini nordostensis* (Sher et al. 2011), we now classify this specimen as a subspecies of *U. rossicus*. Although recovered not in situ, analysis of the local geology and associated mammalian fauna suggests its association with the Olyorian fauna, corresponding to a wide interval of 1.5–0.5 Ma (Sher et al. 2011, Boeskorov et al. 2012, Boeskorov and Baryshnikov 2013). It should be noted that this fauna is subdivided into the Lower Olyorian fauna, which correlates with the upper part of the Matuyama Chron, and the Upper Olyorian fauna, corresponding to the lower part of the Brunhes Chron (Sher et al. 1979). According to Sher et al. (2011), the mandible (IAM No. F-2365) from the Ovrag locality is most likely associated with faunal level "B". This level predominantly contains elements of the Lower Olyorian fauna, including both small and large mammals, although it also includes some admixture of taxa from higher stratigraphic levels, particularly Late Pleistocene forms. In other words, only the early Olyorian and Late Pleistocene components are clearly distinguishable in the Ovrag locality assemblage (Sher et al. 2011). Boeskorov et al. (2012) also support an early Olyorian age for the holotype of *U. r. nordostensis*. This interpretation is further supported by the preservation state of this mandible – black, dense, and heavily fossilized – which is consistent with other Lower Olyorian specimens housed in the collection of the GIN RAS.

The new, previously undescribed material from Irgiz 1 (RMZ No. 02/397-399) includes a fragment of the left hemimandible of a juvenile *U. rossicus*. The Irgiz 1 locality (51° 56′ N, 48° 30′ E; Text-fig. 1) is situated in the Saratov Region. The fauna of small and large mammals from Irgiz 1 belongs to the Khazar faunal complex, dated to the late Middle to early Late Pleistocene (MIS 7–5; Prilepskaya et al. 2019, Rivals et al. 2020). The alveoli of dp3, dp4, m1, and m2 are preserved on the specimen. The canine c1 is preserved at the stage of permanent tooth formation, and is represented by an enamel cap without cementum inside the crown. In addition, a fully formed and well-preserved permanent fourth premolar without roots was extracted from the mandibular body of this specimen. The examined specimen RMZ No. 02/397-399 was 3D-scanned with an Artec Micro 3D scanner operated with Artec Studio 18 software at a resolution of up to 0.015 mm and the accuracy up to 10 μm.

The type series of *U. rossicus* is currently housed at the PIN RAS. This collection was acquired in the first half of the

Text-fig. 1. Map of discussed Eastern European and Asian localities; red: *U. rossicus*, white: *U. kanivetz*.

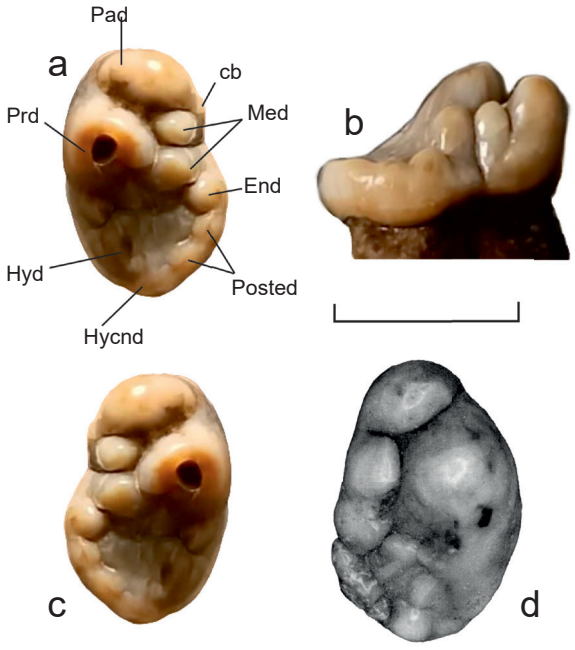
20th century, following the excavation of several *U. rossicus* skeletons by members of the Felitsyn Krasnodar State Historical and Archaeological Museum-Reserve near the Krasnodar city in southern Russia (hereafter referred to as the Krasnodar locality, 45° 02′ N, 38° 59′ E; Text-fig. 1).

Analysis of the geological setting and associated vertebrate fauna indicates a late Middle to early Late Pleistocene age of the deposits yielded the remains of *U. rossicus* (Borissiak 1930, 1932, Baryshnikov 2007). The entire type series was described by Borissiak (1932), but a holotype was not identified. Subsequently, a skull with a mandible (PIN No. 2283/362) was designated as the lectotype for *U. rossicus* (Baryshnikov 1981). The skull and the mandible are articulated, which prevents the study of the occlusal morphology of p4. Therefore, we examined the left lower fourth premolar PIN No. 2283/71 from the same type series. Further comparison was made with a photo of p4 from another mandible of *U. rossicus* (PIN No. 2283/363) provided by Borissiak (1932: 206, tab. IV, fig. 2).

The Imanay Cave collection (IPAE No. 2284) from the Southern Urals near the Nugush River (53° 02′ N, 56° 26′ E; Text-fig. 1) represents the largest known assemblage of *U. rossicus*. This material (IPAE No. 2284) is held at the IPAE. A large sample (20 specimens) of previously unpublished isolated p4 of *U. rossicus* was examined for this study. The rich fossil small mammal fauna of the cave corresponds to the Late Pleistocene (Fadeeva et al. 2022, 2023), while radiocarbon dating of *U. rossicus* bones yielded ages ranging from 46,000 to 26,000 BP, placing the assemblage within MIS 3–2 (Gimranov and Kosintsev 2020, Gimranov et al. 2021, 2023).

For comparison with the large cave bears, we examined p4 of *U. kanivetz* from Ural localities (Text-fig. 1) of Asha 1 Cave (n = 1, IPAE No. 248), Pobeda Cave (n = 3, IPAE No. 467), and Nukatskaya Cave (n = 1, IPAE No. 2964). These collections, stored at the IPAE Museum, originate from Southern Ural natural burial sites of large cave bears (Gimranov and Kosintsev 2022). Radiocarbon dating of the large cave bear remains from these sites indicates an age range of 60,600–26,500 BP, corresponding to the Late Pleistocene or MIS 3–2 (Kosintsev et al. 2016, Danukalova et al. 2020, Gimranov and Kosintsev 2022).

Additional data were obtained from the literature, with particular attention to the material identified as *U. savini*



Text-fig. 2. Lower fourth premolar of *U. rossicus* from Asia. a–c: Ovrag (IAM No. F-2365); a: occlusal view, b: lingual view, c: occlusal view (reversed). d: Berezhekovo (IAET No. 36), occlusal view (reproduced from Baryshnikov and Foronova 2001: fig. 7). Scale bar 10 mm.

rossicus from the latest Middle Pleistocene locality of Mishin Kamik in north-western Bulgaria (Spassov et al. 2017: pl. 2, figs 11–15), and the p4 of *U. rossicus* resembling *U. r. nordostensis*, described from the Berezhekovo segment of the Kurtak geoarchaeological district (Text-fig. 1) in South Siberia, near the Yenisei River (Baryshnikov and Foronova 2001: fig. 7; Text-fig. 2d here). The Berezhekovo deposits were dated to the Middle-Late Pleistocene (Drozdov et al. 2005).

A mass assemblage of the Late Pleistocene small cave bear was also described from Kizel Cave, located on the western flank of the Middle Urals. That material was initially described as a new species, *Ursus uralensis* Vereshchagin, 1973, but was later reclassified as a subspecies, *Ursus rossicus uralensis* (Vereschagin and Baryshnikov 2000, Baryshnikov 2007). It was also included in molecular studies (Barlow et al. 2021). The material is currently housed at the ZIN RAS, but is presently unavailable due to re-examination. Although previous descriptions (Vereschagin and Baryshnikov 2000, Baryshnikov 2007) report a substantial sample of lower fourth premolars (14 specimens) of *U. rossicus uralensis*, these works do not provide the specific morphological features necessary to our analysis of p4, nor do they include photographs of the specimens. Consequently, that material is not considered in the present study.

In descriptions of Pleistocene ursids, researchers employed the terms "spelaeoid" and "arctoid" lineages (Santi et al. 2003, Rabeder et al. 2010, Wagner and Čermák 2012, Santos et al 2014, Marciszak et al. 2019, Pérez-Ramos, 2020). According to Baryshnikov (2007), the "arctoid" and the "spelaeoid" ursids correspond to the subgenera *Ursus* Linnaeus, 1758 and *Spelearctos* E. Geoffroy Saint-Hilaire, 1833 respectively. The most probable common ancestor of the spelaeoid and the arctoid lineages is believed to be *U. etruscus* Cuvier, 1823.

All the specimens were measured and photographed, and the information was entered into a database. The measurements were taken with an engineering calliper at an accuracy of 0.1 mm. Tooth measurements were determined according to Rode (1935) with minor additions.

In this paper, we follow the basic dental terminology by Rabeder (1983, 1989), with some additions and modifications. Following Baryshnikov (2007), for the description of the molarized p4, we primarily adopted the terminology used for molars. In this framework, the main elements include the trigonid, composed of the paraconid, protoconid, and metaconid, and the talonid, which comprises the hypoconid, entoconid, and hypoconulid. We also introduce the term talonid basin.

When describing multicuspid structures – such as those arising from modifications of the main cusps in the p4 of *U. rossicus* – we employ a simplified terminology. For instance, we refer to a protoconid, comprising one, two or multiple cusps (= protoconid complex), or a two-cuspid metacoid (= metaconid complex). This approach is particularly useful when discussing multicuspid formations, where the focus is on topological analogues rather than precise homologies.

Such patterns of cusp multiplication and topological rearrangement are clearly observed in the molarization of the p4 in *U. rossicus*, especially in its most derived morphotypes. Used cusp nomenclature does not reflect the true homology of premolar cusps – which, moreover, remains poorly studied – but is instead based primarily on topological basis.

All dimensions are given in millimetres. All graphs were prepared in Microsoft Excel and StatSoft STATISTICA 6.

Institutional abbreviations

GIN RAS	Geological Institute of the Russian Academy of Sciences (Moscow, Russia)
IAM	Ice Age Museum (Moscow, Russia)
IPAE	Institute of Plant and Animal Ecology, the Ural Branch of the Russian Academy of Sciences (Yekaterinburg, Russia)
MSU	Lomonosov Moscow State University (Russia)
PIN RAS	Borissiak Paleontological Institute of the Russian Academy of Sciences (Moscow, Russia)
RMZ	Regional Museum of Earth Sciences at SSU (Saratov, Russia)
SSU	Saratov State University (Russia)
SIEE RAS	Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences (Moscow, Russia)
ZIN RAS	Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia)

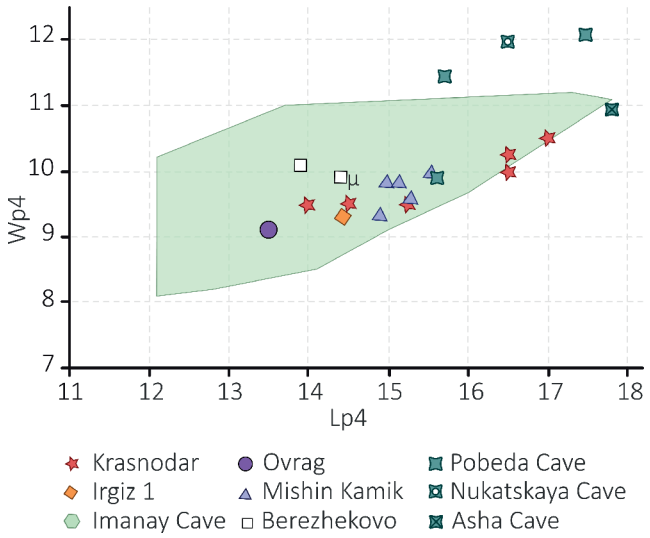
Other abbreviations

cb	cingulid bulge
End	entoconid
Hld	hypoconulid
Hyd	hypoconid
Med	metaconid
Pad	paraconid
Prd	protoconid
TB	talonid basin
L	greatest length
W	greatest width
W tal	greatest talonid width
W tr	greatest trigonid width

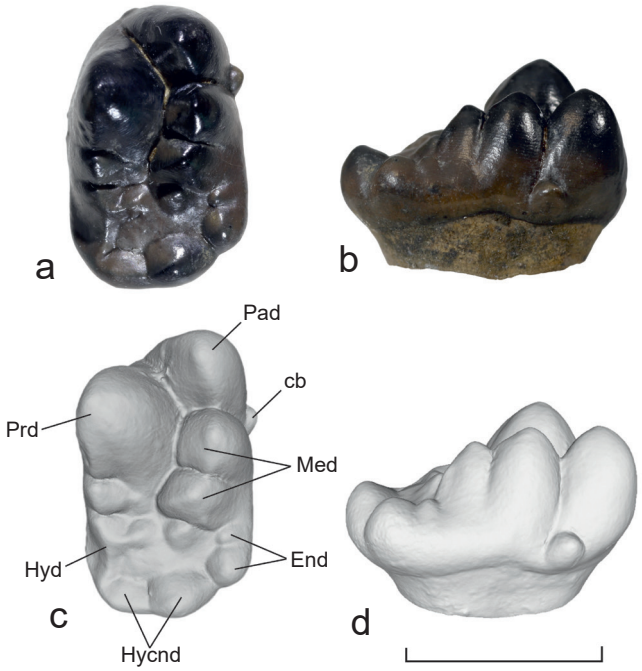
Results

The lower fourth premolar of *U. rossicus* from the Ovrag locality

The fourth premolar (IAM No. F-2365) of *U. r. nordostensis* from the Ovrag locality (Text-fig. 2a–c) falls within the size range observed in both small and large cave bears (Lp4 = 13.50, Wp4 = 9.10) (Text-fig. 3). In occlusal view, p4 exhibits an oval outline, with a lingual concavity ca. opposite to Prd apex, and with a noticeable narrowing of the crown in the distalmost quarter of the tooth. It is slightly wider in the talonid than in the trigonid (W tr = 8.30, W tal = 9.10). The trigonid displays a paraconid, protoconid, and two lingual metaconid cusps. A small basal cingulid bulge



Text-fig. 3. Ratio of width (W) and length (L) of fourth lower premolar of small and large cave bears; μ – mean value for Imanay Cave. Data after Borissiak 1932, Baryshnikov and Foronova 2001, Spassov et al. 2017, our data.



Text-fig. 4. Lower fourth premolar of *U. rossicus* from Irgiz 1 (RMZ No. 02/397-399). a, b: natural view, c, d: scanned view; a, c: occlusal view, b, d: lingual view. Scale bar 10 mm.

is also present at the lingual border between the paraconid and the metaconid. An unexpectedly large, massive, and unicuspid paraconid is located mesiolingually relative to the other cusps and strictly mesial to the protoconid, from which it is separated by a distinct groove. The large, unicuspid protoconid occupies three-quarters of the trigonid's transverse space and bears a mesial ridge.

The metaconid consists of two cusps, both of which are well individualised, round in cross-section, and without crests. In lingual view, its cusps are almost equal in size and height, resembling columns with a vertical groove between them. These cusps are also tightly pressed against the distal wall of the paraconid, separated from it by another vertical groove, but this one is much weaker (Text-fig. 2b). In addition, they are considerably lower than the paraconid and the protoconid. The p4 talonid is well-developed, elongated, and mesially widened. In the occlusal view, the distal part of the talonid is noticeably narrower. The hypoconid is ridge-like, the hypoconulid is weak, and the entoconid is distinct. Behind the entoconid, there are two additional entoconid small cusps. The entoconid lacks crests but protrudes lingually. A small space in the lingual part of the talonid likely corresponds to the talonid basin.

The lower fourth premolar of *U. rossicus* from the Irgiz 1 locality

The fourth premolar of *U. rossicus* from Irgiz 1 (RMZ No. 02/397–399) falls within the size range observed in small and large cave bears (Lp4 = 14.43, Wp4 = 9.27) (Text-fig. 3). Its crown has a rectangular outline with rounded corners. The trigonid and the talonid widths are nearly identical (W tr = 9.17, W tal = 9.27). The large, massive, unicuspid paraconid is situated in the mesiolingual part of the crown and is separated from the protoconid by a deep groove. The apex of the paraconid is positioned mesiolingually to the apex of the protoconid, with its mesial margin lying anterior to the mesial edge of the protoconid (Text-fig. 4).

Deep basal grooves separate the largest buccal element from the other cusps. The distal cusp of protoconid is significantly smaller than the mesial one, bearing a distal crest directed toward the hypoconid. The mesial crest of the protoconid is poorly developed. The protoconid base occupies two-thirds of the trigonid width. The metaconid is distinctly bicuspidate, with the distal cusp slightly smaller than the mesial one, and its axis aligned relative to the tooth's long axis. The distal cusp has a distinct tip, from which a weak transverse crest extends to the medial part of the trigonid. The boundary between the trigonid and the talonid is well-defined and marked by a transverse groove behind the distal cusps of the metaconid and the protoconid. The talonid is elongated and widened. The large, well-developed hypoconid is distinctly positioned buccally and bears three crests: mesial, distal, and medial. The entoconid is bicuspid, situated opposite the hypoconid, with a small anterior and larger distal cusp, both occupying a strictly lingual position and having no crests. Between the hypoconid and the entoconid lies a flat space with a few cusps, which can be called a talonid basin. Two distinct cusps are situated distally to the hypoconid and the entoconid, potentially corresponding to hypoconulid cusps commonly observed in molars. These cusps are larger than the entoconid, each with a distinct apex and two crests extending transversely to the disto-mesial tooth axis. In lingual view, the trigonid rises significantly above the talonid. The paraconid is tightly pressed against the metaconid, with their edges converging for almost three-quarters of the cusps' height. All the lingually visible cusps are slightly inclined mesially, with their lengths and heights gradually decreasing distally. Additionally, a small but well-pronounced cusp is visible at the base of the paraconid, likely of a cingulid origin (Text-fig. 4c, d).

The lower fourth premolar of *U. rossicus* from the Krasnodar locality

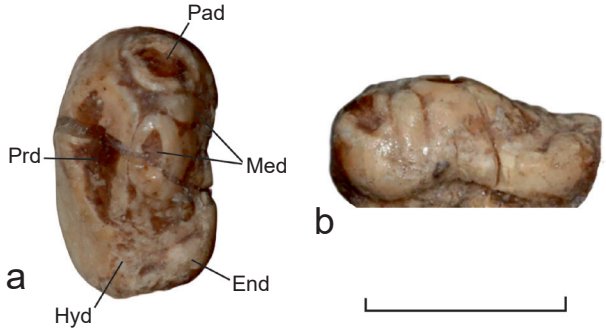
The fourth premolar of *U. rossicus* from the Krasnodar locality falls within the size range observed in both small and large cave bears (Lp 4 = 13.50, Wp4 = 9.10) (Text-fig. 3). The studied premolar from the left hemimandible of PIN No. 2283/71 (Text-fig. 5) is heavily worn on the trigonid cusps. Its crown has a rounded rectangular outline, while the paraconid has a sub-triangular outline. The paraconid is positioned mesiolingually and is separated from the other cusps by a deep groove. Its mesial margin is located anterior to the mesial edge of the protoconid

The protoconid is the largest cusp of the tooth, occupying two-thirds of the transverse width of the dental crown. The metaconid consists of two cusps: a small mesial cusp and a larger second cusp comparable in size to the paraconid. Both the paraconid and the metaconid are smaller than the protoconid. The latter cusp lacks additional pronounced elements. The boundary between the trigonid and the talonid is indistinct, and details of the talonid structure are poorly visible. The talonid bears a higher hypoconid and a lower entoconid. No other additional cusps are present on the talonid, although the talonid itself is well-developed. In the lingual view, the trigonid rises significantly above the talonid.

According to the drawing and the description by Borissiak (1932: 206, tab. IV, fig. 2), another specimen from the Krasnodar collection, PIN No. 2283/363 displays a more advanced stage of molarisation of p4, surpassing all the other specimens examined in this study. The specific features of molarisation observed in the type series specimens will be dealt with further in the Discussion.

The lower fourth premolar of *U. rossicus* from the Imanay Cave

In *U. rossicus* from the Imanay Cave, the multiple examined p4s (n = 20, Lp4 = 14.43, Wp4 = 9.27, on average) fall within the size range observed in both small and large cave bears (Text-fig. 3). Most of their crowns have a rounded rectangular outline, although some have a nearly oval shape. The paraconid is prominent, but does not exceed the protoconid in size. It is separated from the protoconid by a deep groove and, except in a few instances, lacks additional cusps. As in most specimens of *U. rossicus*, the paraconid is typically mesiolingually positioned, occasionally adopting a mesial position, or less frequently, a strictly lingual one (Text-fig. 6j, k). Regardless of its placement, the mesial edge of the paraconid is nearly always situated anterior to the mesial border of the protoconid (Text-fig. 6).



Text-fig. 5. Lower fourth premolar of *U. rossicus* from Krasnodar (PIN No. 2283/71). a: occlusal view, b: lingual view. Scale bar 10 mm.

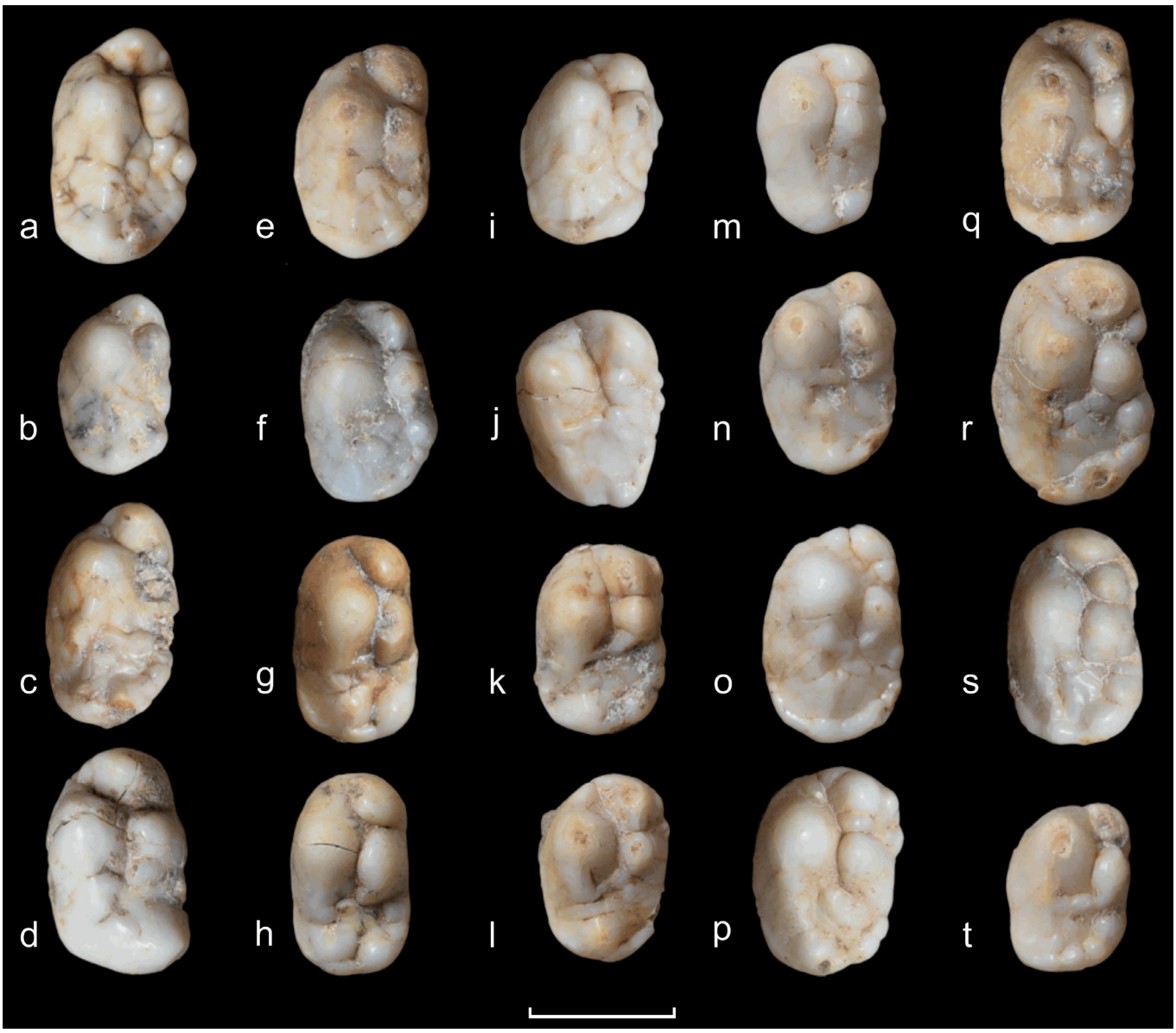
The protoconid is the largest cusp on the p4, with distal additional cusps occurring in rare cases. Its base occupies two-thirds of the trigonid width in 75 % of cases, while in the remaining cases, it accounts for half the width. The protoconid bears an underdeveloped mesial crest and a distal crest oriented toward the hypoconid. The metaconid is typically unicuspid, although small mesial (Text-fig. 6m, o, p, s) and distal (Text-fig. 6a, d, l, n) cusps may occasionally be present (Text-fig. 6). The metaconid has a disto-medial crest, which is sometimes connected to the distal crest of the protoconid. The boundary between the trigonid and the talonid is not well-defined. The talonid is generally well-developed, often occupying half of the occlusal surface. The hypoconid and the entoconid are present in most specimens, while a talonid basin is observed in 50 % of the examined teeth. A large hypoconid is sometimes centrally positioned, and the entoconid often appears as small cingulid cusps, with their number varying among specimens. In lingual view (Text-fig. 7), the trigonid rises above the talonid. The paraconid is tightly pressed to the metaconid, their edges converging except at the uppermost part, where they diverge. The metaconid matches the paraconid in length. In cases when the metaconid bears secondary cusps, these are notably smaller and lower than the main cusp (Text-fig. 7).

The lower fourth premolar of *U. kanivetz* from caves Asha 1, Pobeda, and Nukatskaya

The multiple examined p4s (n = 5, Lp4 = 14.43, Wp4 = 9.27, on average) of the large cave bear (*U. kanivetz*) from the Southern Urals caves, Asha 1, Pobeda, and Nukatskaya (hereafter referred to as APN), fall within the size range of variation observed in both large and small cave bears (Text-fig. 3).

In occlusal view, the crown of p4 has a slightly rounded rectangular outline. The trigonid pattern is divided into lingual and buccal cusps, occupying a whole occlusal surface of trigonid (Text-fig. 8). The paraconid is located on the lingual side of the crown. It is separated from the protoconid by a deep groove. The paraconid is large, occasionally bicuspidate, but always smaller than the protoconid. The mesial margins of the paraconid and protoconid are approximately at the same mesial level. The protoconid is the largest cusp of the p4. It lacks additional cusps and bears a well-developed mesial and distal crest. Both characters are plesiomorphic in comparison to the p4 of *U. rossicus*.

The base of the protoconid occupies two-thirds of the trigonid's width, with its distal crest positioned overall more centrally than in *U. rossicus*. The metaconid is equal in size to the paraconid, and its distal crest is oriented medially, towards the distal edge of the protoconid. The boundary between the trigonid and the talonid is poorly defined. In contrast to *U. rossicus*, the talonid of *U. kanivetz* is less developed. The hypoconid is a weak crest positioned centrally, while the other talonid cusps are poorly developed



Text-fig. 6. Lower fourth premolar of *U. rossicus* from Imanay Cave, occlusal view. a: IPAE No. 2284/5638, reversed; b: IPAE No. 2284/6603; c: IPAE No. 2284/5172; d: IPAE No. 2284/4588, reversed; e: IPAE No. 2284/6187, reversed; f: IPAE No. 2284/5003, reversed; g: IPAE No. 2284/6809, reversed; h: IPAE No. 2284/744; i: IPAE No. 2284/5087; j: IPAE No. 2284/6692, reversed; k: IPAE No. 2284/2395; l: IPAE No. 2284/3454; m: IPAE No. 2284/3343; n: IPAE No. 2284/5326; o: IPAE No. 2284/6261; p: IPAE No. 2284/4443; q: IPAE No. 2284/5994, reversed; r: IPAE No. 2284/745; s: IPAE No. 2284/3568; t: IPAE No. 2284/6811. Scale bar 10 mm.

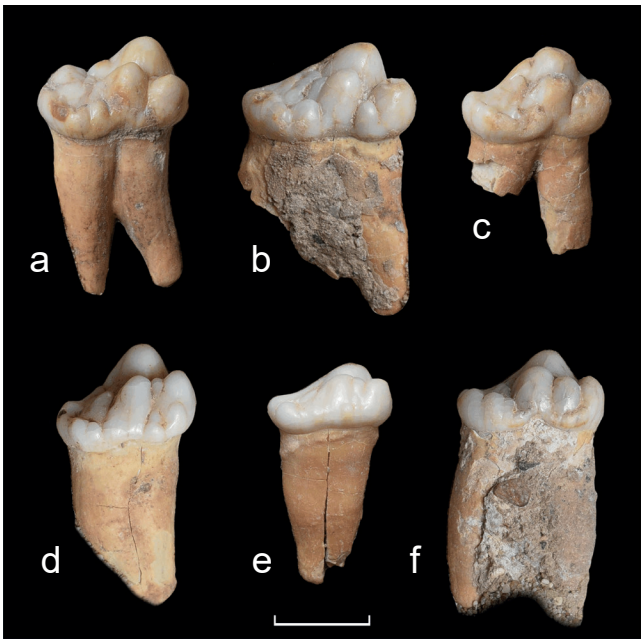
or absent. In lingual view, the trigonid rises significantly above the talonid. In contrast to *U. rossicus*, the paraconid and metaconid are more widely separated, coming into contact only at their basal parts.

Discussion

Evolution of the lower fourth premolar of *U. rossicus* in the Early, Middle, and early Late Pleistocene

The hemimandible of *U. r. nordostensis* IAM No. F-2365 from the Ovrag locality near the Cherskiy town represents the oldest known record of a small cave bear in Eurasia, with age identified as the terminal Early Pleistocene (Boeskorov et al. 2012, this study). Its plesiomorphic characters include a very high mandibular body, a downward-extending symphysis forming a pronounced "chin" (similar to some deningeroid bears), nearly equal lengths of m1 and m2, and a poorly developed m2 talonid (Sher et al. 2011). Additional basal traits include an almost linear incisor row and an incomplete checkerboard arrangement of the incisors, in contrast to other spelaeoid bears. Its p4 retains the crown outline similar to the deningeroid group of bears, such as a subtriangular outline of the distal crown, contrasting with sub-rectangular or sub-square shapes seen in other cave bears. The ancestral traits of p4 include an anterior placement of the paraconid relative to the protoconid, small and low metaconid cusps, an anterior protoconid crest, and a weak ridge-like hypoconid on the talonid (Text-fig. 2).

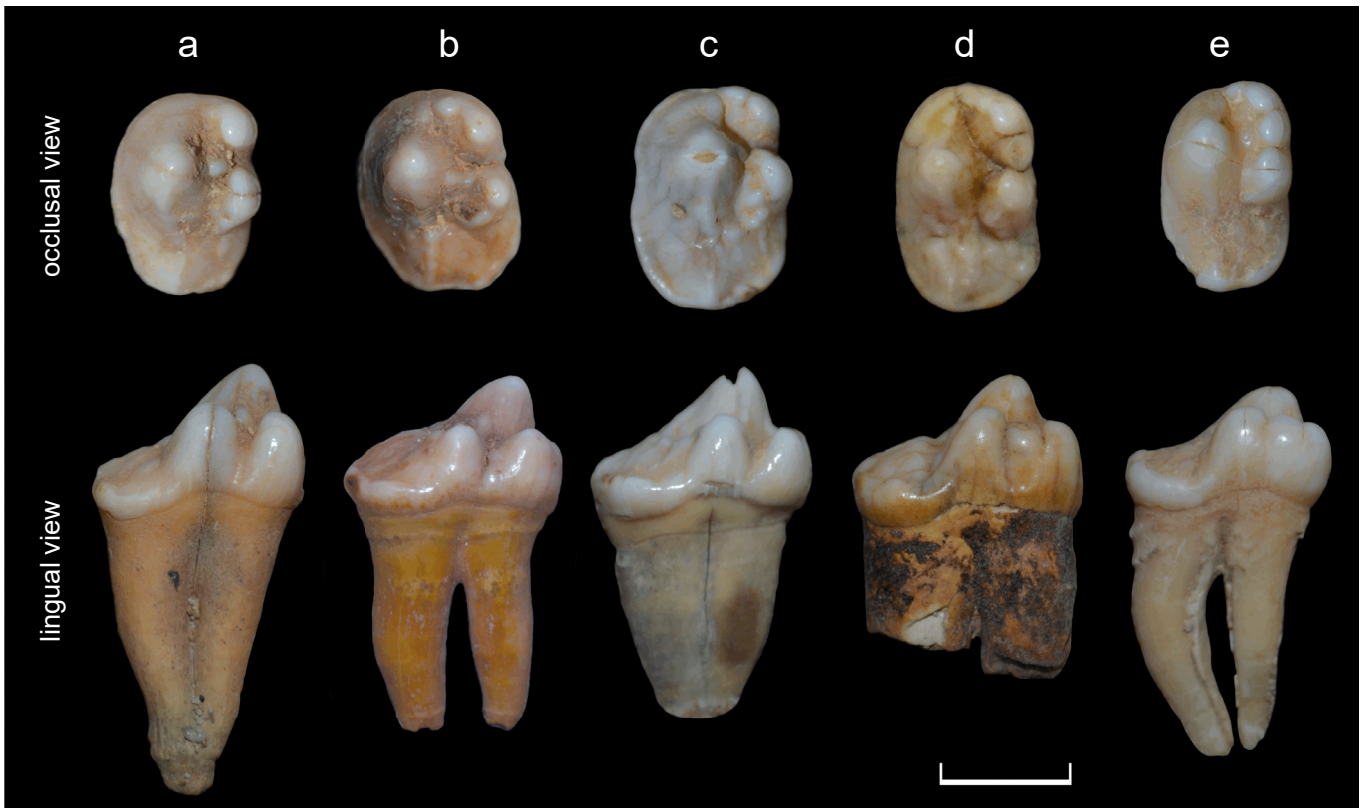
The derived features of p4 IAM No. F-2365 include a massive paraconid, with the distal wall closely appressed to the double metaconid, a complete set of talonid cusps, a distinct buccal position of the hypoconid, and a space



Text-fig. 7. Lower fourth premolar of *U. rossicus* from Imanay Cave, lingual view. a: IPAE No. 2284/5638, reversed; b: IPAE No. 2284/745; c: IPAE No. 2284/6187, reversed; d: IPAE No. 2284/4443; e: IPAE No. 2284/3343; f: IPAE No. 2284/3568. Scale bar 10 mm.

between the buccal and the lingual talonid cusps. Notably, the advanced arrangement of the tightly clustered lingual trigonid cusps is an apomorphy of *U. rossicus*, whereas the p4 of *U. savini* exhibits widely spaced lingual cusps (Baryshnikov 2007: fig. 92) – a primitive feature. Based on this character, we consider the subspecies *nordostensis* within the species *U. rossicus*, rather than within *U. savini*, as was proposed by Sher et al. (2011), and supported by other researchers (Boeskorov et al. 2012, Boeskorov and Baryshnikov 2013). In summary, this analysis highlights a unique, mosaic character of p4 in *U. r. nordostensis*. Perhaps a further detailed study of all the cheek teeth will allow us to consider this form as an independent species within the group of small cave bears.

In South Siberia, remains of *U. rossicus* were documented from the Berezhekovo section (Kurtak geoarchaeological district in the Yenisei basin; Baryshnikov and Foronova 2001, Malikov 2018). The most informative specimen from Berezhekovo was described by Baryshnikov and Foronova (2001: fig. 7) as *U. rossicus*. Its exact age remains uncertain, because the material originates from Quaternary eroded brown loams found in the section's basement and on the river beach. Baryshnikov (in Sher et al. 2011) noted that the p4 from Berezhekovo is more similar to that of *U. r. nordostensis* than to typical *U. rossicus* from the Krasnodar collection. The current analysis has identified that the tooth from Berezhekovo (Text-fig. 2d) has both primitive and advanced features, many of which were not given sufficient attention in the original description. Indeed, the p4 from Berezhekovo retains some primitive characteristics, such as the paraconid situated strictly mesially to the protoconid, and the hypoconid situated relatively centrally. Unlike other *U. rossicus* and similarly to *U. r. nordostensis*, it also has an oval crown outline. However, the tooth from Berezhekovo is more derived than the Olyorian specimen in having more bunodont type of trigonid cusps. The combination of these features suggests a Middle Pleistocene rather than Late Pleistocene age of the specimen.



Text-fig. 8. Lower fourth premolar of *U. kanivetz* from Southern Urals. a: IPAE No. 467/11733, from Pobeda Cave, reversed; b: IPAE No. 2964/277, from Nukatskaya Cave, reversed; c: IPAE No. 467/10845, from Pobeda Cave; d: IPAE No. 248/10977, from Asha 1 Cave; e: IPAE No. 467/10847, from Pobeda Cave. Scale bar 10 mm.

The next stage of the evolution of p4 in small cave bears is illustrated by material from the Irgiz 1 locality dated within MIS 7–5 (Text-fig. 4**)**. Compared to the premolar of *U. r. nordostensis* from Ovrag and the premolar from Berezhekovo, this p4 has many advanced traits and demonstrates a high level of molarisation. Its derived characteristics include a rounded rectangular outline, a relatively low and massive paraconid, a bicuspidate protoconid complex, a very large tricuspidate metaconid complex, and an extremely complicated talonid with small cusp-like bulge in its basined central part. Moreover, the talonid includes a hypoconulid space containing two large distal cusps – a feature unique to small cave bears, rarely found even in this group and never found in large cave bears (*U. spelaeus* s. l. in Rabeder 1983, 1989).

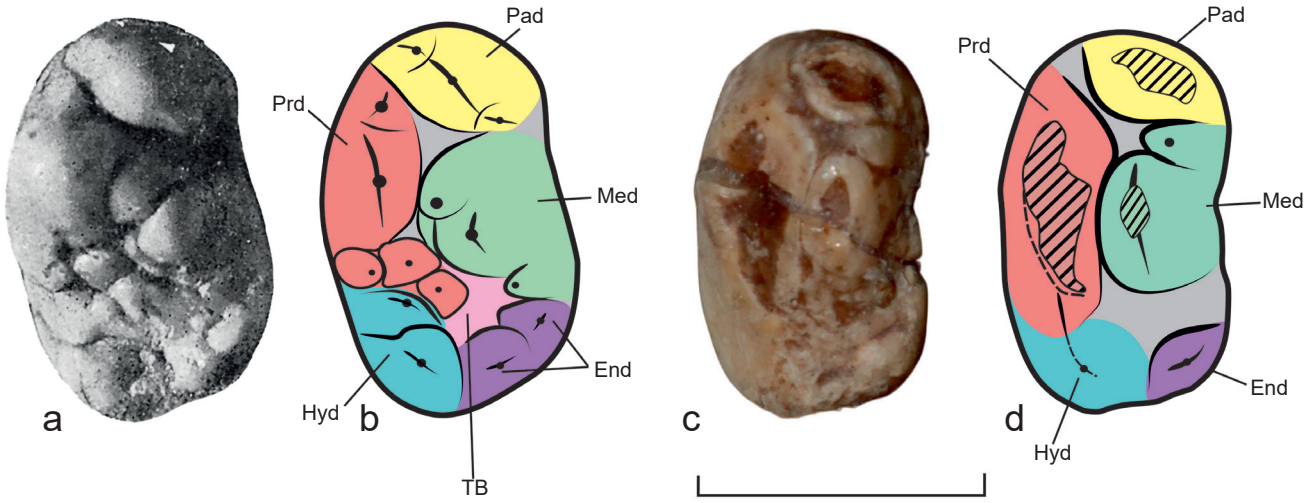
Nevertheless, an even more multicuspidate structure of p4 was observed in specimen PIN No. 2283/363 from the Krasnodar type collection, which is close in age to the fauna from Irgiz 1. As noted above, only four specimens of p4 are known among the type series material, two of which remain unavailable for study. Specimen PIN No. 2283/71 (Text-figs 5, 9c–d) was described in the Results section, and exhibits features typical of the average p4 morphotype of *U. rossicus*. Analysis of the most specialised p4 (PIN No. 2283/363; Text-fig. 9a–b) was carried out only due to the detailed description and the figure provided by Borissiak (1932: tab. IV, fig. 2). This specimen demonstrates a notably higher level of trigonid molarisation (Text-fig. 9a, b), even compared to the highly specialized p4 from Irgiz 1 (Text-fig. 4). Its morphological features include a tricuspidate paraconid complex, bicuspidate metaconid complex, and quadricuspidate protoconid complex.

The talonid is composed of a double hypoconid and a series of entoconid cusps. However, the most distal talonid cusps can probably be classified as hypoconulids, and the space between the buccal and the lingual cusps may be interpreted as the talonid basin. Consequently, the Krasnodar type collection includes a specimen with the most advanced p4 morphology (PIN No. 2283/363) and a specimen with the morphology of p4 typical of *U. rossicus* (PIN No. 2283/71). Besides, Borissiak (1932) also noted the presence of specimens within the type series that display a more simplified morphotype of p4.

In Southern Europe, remains of small cave bears were described from Mishin Kamik in Bulgaria (as "*U. savini rossicus*"), dated to the very end of the Middle Pleistocene or the beginning of the Eemian (Spassov et al. 2017). The collection includes five specimens of the lower fourth premolar. Their average size (Lp4 = 15.1, Wp4 = 9.7) falls within the range of variability of this tooth in small and large cave bears (Text-fig. 3). According to Spassov et al. (2017), "the Mishin Kamik bear shares its specific characteristics with *U. rossicus* from the loess of Krasnodar and both samples (KRD and MK) must represent the same taxon". We fully support the identification of the Bulgarian small cave bear as *U. rossicus*, but we would like to emphasize certain details of the morphology of its p4, which demonstrate the main apomorphies of *U. rossicus*: sub-rectangular outlines of the crown, paraconid with the distal wall closely appressed to the double-cusped metaconid, and a fairly complicated talonid. Similar to other *U. rossicus*, it retains the mesial position of the anterior margin of paraconid relative to the anterior margin of the protoconid, and in some cases demonstrates a slightly narrowed distal edge of the talonid (Spassov et al. 2017: pl. 2, fig. 15a). However, we did not observe among the Bulgarian specimens any highly molarised p4, present in the coeval populations of small cave bears from Irgiz 1 and Krasnodar.

Evolution of the fourth premolar of *U. rossicus* at the end of the Late Pleistocene

The most representative samples of p4 (20 specimens; Text-figs 6, 7) of *U. rossicus* originate from the Imanay Cave and date to the end of the Late Pleistocene, corresponding to the MIS 3–2 interval (Gimranov et al. 2021, 2023). To evaluate the evolutionary stage of p4 in these bears, we estimated the frequency (%) of occurrence of some traits.



Text-fig. 9. Lower fourth premolar of *U. rossicus* from Krasnodar, occlusal view. a, b: p4; PIN No. 2283/363 (reproduced from Borissiak 1932: tab. IV, fig. 2); c, d: p4; PIN No. 2283/71. Scale bar 10 mm.

In 60 % of the Imanay bears, the paraconid was more shifted lingually than in the bears from the Ovrag, Irgiz 1, and Krasnodar localities, and this trait can be considered a derived character. Moreover, in one tooth, the paraconid and metaconid are positioned completely lingually (Text-fig. 6k), which is typical of large cave bears. Additional derived features of the bears from Imanay include a large, massive hypoconid, often shifted buccally; the entoconid occasionally appears as small cingulid cusps, and in most cases (65 %), a subrectangular outline of the crown.

Nevertheless, several ancestral traits persist in the Imanay specimens. These include the presence of a distal crest on the metaconid (80 %), slightly complicated trigonid cusps (30 %), a single hypoconid without additional elements (65 %), and an undeveloped talonid basin (60 %). Additionally, the talonid frequently displays small cingulid elevations on the distolingual side of the crown, rather than fully developed entoconid cusps or other accessory elements. Furthermore, the teeth retain the paraconid's mesial margin positioned ahead of the protoconid's mesial edge, an ancestral trait consistently observed in all *U. rossicus* specimens.

Consequently, p4 in *U. rossicus* from Imanay Cave appears more simplified and lacks the highly specialised morphotypes observed in the Middle Pleistocene forms. This phenomenon is challenging to interpret, given that the Imanay collection represents the most recent population of *U. rossicus*, compared to the previously discussed samples. However, as the analysis demonstrates, some transitional Middle-Late Pleistocene populations, such as those from Bulgaria, also lack highly molarised morphotypes, while the type series from Krasnodar includes specimens exhibiting both high and moderate levels of specialisation in the lower fourth premolar. Based on these findings, it can be hypothesised that the most complex morphotypes have not yet been identified in the Imanay collection. Alternatively, it cannot be excluded that during the evolutionary processes in the Late Pleistocene, the highly molarised p4 became less advantageous for the dietary adaptations of small cave bears, leading to a significant deceleration in its molarisation. However, it is possible that a secondary simplification of features took place here. Another suitable scenario is the persistence of a distinct lineage of small cave bears in the Ural region during the late Late Pleistocene (Text-fig. 10).

Text-fig. 10. *U. rossicus* near entrance to Imanay Cave. Reconstruction by Polina Mitroshkina.

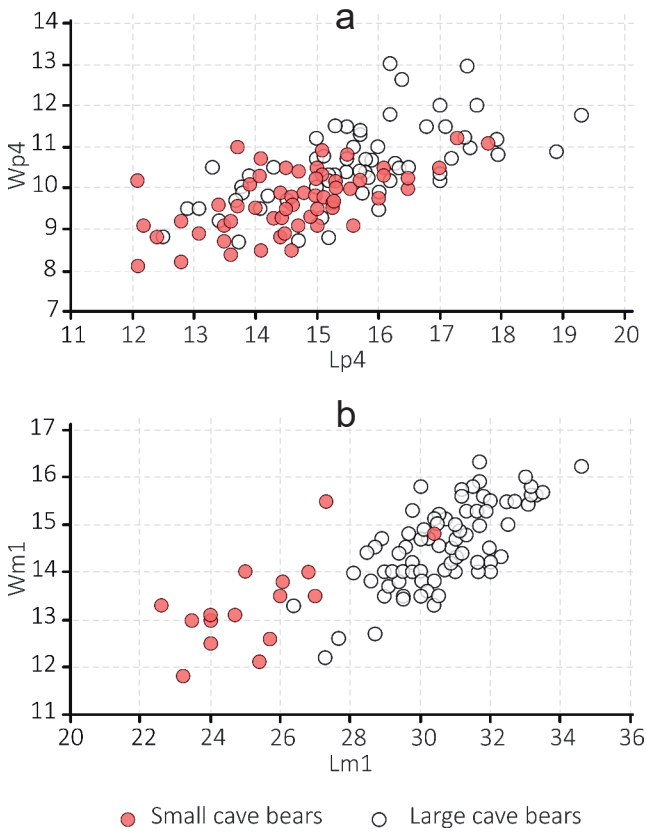
Evolution of the lower fourth premolar of *U. spelaeus* s. l. and the development of two different directions in molarization of this tooth in large and small cave bears

As previously noted, considerable attention was devoted to the study of the structure of the lower fourth premolar in large cave bears (Rabeder 1983, 1989, Torres 1984, Baryshnikov 1998, 2007). Based on the analysis of the frequency of p4 morphotypes in *U. spelaeus* s. l. from Europe (Rabeder 1983, 1989), the majority of examined specimens exhibited a simple structure of p4, characterised by a unicuspid protoconid, paraconid, and metaconid, with a centrally positioned hypoconid. We also observed all the main structural features of the p4 in large cave bears, using *U. kanivetz* from the Urals as an example. A distinctive feature of these bears is the complete lingual shift of the paraconid, the position of which becomes aligned with the metaconid. In this case, the anterior margins of the paraconid and protoconid are positioned at the same level, occupying the anteriormost part of the occlusal surface. Another derived trait is the sub-square (occasionally subrectangular) outline of the tooth, with no distal or mesial narrowing. However, similar to other large cave bears, *U. kanivetz* retains certain primitive traits. In lingual view, the paraconid and metaconid are widely separated, and in most cases, their bases are not in contact. The fourth premolar also preserves a mesial crest on the protoconid. The short talonid is characterised by a centrally positioned hypoconid, without any additional cusps (Text-fig. 8). In general, p4 of *U. kanivetz* from the Urals exhibits a simple structure of the main trigonid cusps, occasionally complicated by a bicuspidate paraconid (Text-fig. 8b, e). Similar observations were made by Kosintsev and Sataev (2005: 133), who studied the morphology of p4 in *U. kanivetz* from the locality Asha 1.

Conclusion

Based on the current morphological analysis, it is important to highlight that the significant differences in the structure of the fourth premolars of large and small cave bears result from distinct evolutionary pathways in their molarization processes. Large cave bears (*U. spelaeus* s. l.) retain more primitive characteristics, such as the lack of a pronounced complication in the cusp structure on the trigonid and a poorly developed talonid. However, they also acquire a key apomorphic feature absent in *U. rossicus*: a complete displacement of the paraconid to the lingual side of the crown. In contrast, small cave bears (*U. rossicus*) display more apomorphic traits, including a complex structure of the trigonid and talonid cusps, and a developed talonid.

As a result, the p4 of *U. rossicus*, in comparison with early deningeroid forms, exhibits increased linear dimensions relative to the other cheek teeth, primarily due to the development of the talonid. In contrast to *U. rossicus*, the linear dimensions of p4 in large cave bears did not increase significantly, as their talonid retained primitive structural features. These modifications help explain the phenomenon where the length values of p4 overlap between large and small cave bears, while the linear dimensions for m1 in these two forms are distinct from each other (Text-fig. 11).



Text-fig. 11. Ratio of width (W) and length (L) of lower fourth premolar (a) and lower first molar (b) of small and large cave bears. Data after Rabeder et al. 2004, Baryshnikov 2007, Boeskorov and Baryshnikov 2013, Santos et al. 2014, and our data.

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