



FIRST RECORD OF THE “SMALL CAVE BEAR” IN BULGARIA AND THE TAXONOMIC STATUS OF BEARS OF THE *URSUS SAVINI* ANDREWS – *URSUS ROSSICUS* BORISSIAK GROUP

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Abstract: The discovery of rich, well preserved skull material in the latest Middle Pleistocene deposits of Mishin Kamik cave (N-W Bulgaria) presents an opportunity for a new analysis of the taxonomy and the phylogeny of the so called “small cave bears”. Not all the small cave bears known would have necessarily had a common origin, the size decrease could be related in a number of cases to a parallelism. The bear from Mishin Kamik is identical with “*Ursus rossicus*” BORISSIAK from Krasnodar (S. Russia). Both these samples must be referred to *U. savini* ANDREWS from Bacton near Cromer (England). The specimens from Krasnodar and Mishin Kamik could be classified as *U. sa. rossicus*, a late form of the species. This species may have affinities with some Middle Pleistocene Siberian forms. *U. savini* is a small but very robust spelaeoid bear which is more advanced in a number of features than *U. deningeri*. In several aspects it attained the evolutional adaptations of the cave bears of the *U. spelaeus-U. ingressus* group and represents an independent lineage of spelaeoid bears. The Mishin Kamik population was adapted to a mosaic landscape of forests and open areas in hilly terrain. This bear had well developed grazing adaptations but had weak motor abilities.

Key words: *Ursus savini*, *Ursus savini rossicus*, small cave bears, *Ursus deningeri*, cave bears taxonomy, Middle Pleistocene

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Introduction

Remains of the so called cave bears are among the most common large mammal fossils of the Middle and Late Pleistocene of Europe and there are many publications related to them (see Torres 1988, Kahlke 1999, Baryshnikov 2007, Wagner 2010 and references therein). In spite of the abundant material and the extensive literature, the taxonomy and evolution of spelaeoid bears of the genus *Ursus* remain unclear in detail and opinions are still controversial on a number of points. Moreover, the modern ancient-DNA (aDNA) methods and investigations unexpectedly showed that the diversity and phylogeny in the aforementioned group are more complicated than previously assumed (Rabeder et al. 2004, Pacher et al. 2009, Stiller et al. 2014).

Unlike the case of the “ordinary” giant and late cave bear *Ursus spelaeus* ROSENmüller, 1794 (to which, it seems, we have to add a separate evolutionary line *Ursus ingressus*

RABEDER et al., 2004), the remains of the so called “small” and more archaic cave bears such as *Ursus savini* ANDREWS, 1922, *Ursus “rossicus”* BORISSIAK, 1930, *Ursus “uralensis”* VERESHCHAGIN, 1973, *Ursus “ladinicus”* RABEDER et al., 2004 are rare and their taxonomy remains obscure and rather controversial (Mazza and Rustioni 1994, Baryshnikov 2006, 2007, Pacher et al. 2009, Rabeder et al. 2010, Wagner and Čermák 2012 and references therein). The discovery of rich, well preserved skull material in the Mishin Kamik cave (N-W Bulgaria) provided the opportunity for a new analysis of the taxonomy and phylogeny of the “small cave bears”.

The site of Mishin Kamik

The Mishin Kamik cave is situated in the Fore-Balkan region of North-Western Bulgaria, in lower Cretaceous limestones, on the right slope of the Ogosta river, in the area

of Prevala village. The first excavations were in 2013. The cave deposits are represented mostly by clays and fragments of different sizes from the limestone of the cave itself. They are covered by a calcareous crust which becomes thicker, up to 25 cm, in some of the more interior areas. The cave bear remains were found in brown-reddish clays, cemented in some places by cave carbonates (Ivanova et al. 2014). Also discovered at this time, in all the four trenches prepared in the cave, a concomitant fauna represented by: *Panthera fossilis* (a late stage of the species), *Vulpes vulpes*, *Vulpes lagopus*, cf. *Cuon* sp., *Canis lupus*, *Ursus* cf. *thibetanus*, cf. *Cyrnaonyx antiqua*, *Mamuthus* sp., Rhinocerotidae indet., *Equus hydruntinus*, *Megaloceros* sp., *Cervus elaphus*, ? *Dama* sp., *Hystrix* sp., Caprinae indet. (Ivanova et al. 2014, Gurova et al. 2015, 2016, 2017). *U. thibetanus* CUVIER, 1823 and *Cyrnaonyx antiqua* have a Middle Pleistocene to Eemian distribution in Europe. The presence of fossils of a late, relatively small form of *Panthera (Leo) fossilis* (see Marciszak et al. 2013, Sotnikova and Foronova 2014) gives reason to assume a very late Middle Pleistocene age for the bear sample. This is in accordance with the preliminary results from Uranium-Thorium dating of a stalagmite from the cave: a number of absolute dates were obtained within the interval between 143.1–85.6 ka, but at the moment they cannot be strictly correlated with the level containing the bear skulls/remains and it could be closer to the older date (Gurova et al. 2016). Bearing in mind the preliminary data from the biochronological and absolute dating, we could suggest the levels with the bear skulls to have an age near to the end of MIS 6 or the very beginning of MIS 5. The fauna and the pollen (Gurova et al. 2017) indicate a mosaic landscape of forests and open areas.

Material and methods

The cave bear sample described here comes from Mishin Kamik cave, Trench 1 and was collected during three field seasons (2013 – 2015) (Ivanova et al. 2014, Gurova et al. 2015, 2016). It consists of 7 skulls of adult cave bears (males: Nos FM 3112, FM 3113, FM 3114, FM 3115, FM 3386; females Nos FM 3111, FM 3385), and some postcranials, mostly long bones: humeri, ulna, radius, femur, and tibia. Only two incomplete metapodials have been found. There are a few isolated cave bear teeth.

Measurements were taken following Baryshnikov (2007) for the teeth and skull, and following Torres (1988) for the postcranials. The glabella measurements were taken following Santos et al. (2014). All measurements are in mm. For comparison published data (Borissiak 1932, Zapfe 1948, Mottl 1964, Schütt 1968, Rabeder 1989, 1999, Nagel et al. 2005, Athen 2007, Baryshnikov 2007, Santos et al. 2014) were used plus personal observation, as well as the comparative osteological collection of the National Museum of Natural History, Sofia. The measurements of the Bacton skull were kindly provided by Dr. Martina Pacher (University of Vienna).

A small sample (two male skulls) were scanned using a Nikon Metrology XT H 225 industrial CT scanning system. During analysis the specimen was rotated through 360° and the projections were recorded on a Varian 2520 flat panel

detector with 0.127 mm pixel size. The following settings were used for the analysis: voltage 103 KV, current 110 µA. As a result, 2501 projections per scan were collected using a frame rate of 500 ms. Post processing of the raw micro-CT data included its reconstruction using Nikon Metrology CT Pro 3D software and visualization using VGStudio MAX 2.2. Due to the large size of the specimens, a region of interest CT scan was performed. For the first specimen four acquisitions were performed. During each acquisition approximately one quarter of the object was scanned. After reconstruction the four volumetric models were joined together, with no overlap. For the second specimen three acquisitions were performed. The shape of the specimens were digitized by 3D laser scanning using a Creaform VIUscan color laser scanning system. The polygonal models with resolution of 0.4 mm were exported in STL format using Creaform VXElements software.

Capital letters are used for upper teeth and lower case letters for lower teeth.

Abbreviations

BAC – Bacton; CHR – Cherskiy; CT – Conturines cave; ERH – Einhornhöhle; GS – Gamssulzen cave; GT - Goyet; HH – Hundsheim; KD I – Kudaro I; KD III – Kudaro III; KIZ – Kizel cave; KRD – Krasnodar; MK – Mishin Kamik cave; MOS – Mosbach-Sande; NER – Nerubajskoe; RH – Repolust cave; PTR – Petralona cave; SH – Sima de los Huesos; ZLH – Zoolithenhöhle-Spalte.

Systematic palaeontology

Order Carnivora BOWDICH, 1821

Family Ursidae FISCHER, 1814

Genus *Ursus* LINNAEUS, 1758

Ursus savini ANDREWS, 1922

Ursus savini rossicus BORISSIAK, 1930

E m e n d e d d i a g n o s i s . A spelaeoid bear with small sized but very robust skull: extremely short and broad in the zygomatic arches. The skull (especially in males) bulges significantly in the frontal region, and has a relatively high neurocranium. The muzzle is very short. The frontal sinuses extend backward significantly. The occipital is very deep in the area of the external occipital protuberance. The lingual morphology of P4 is simple, the protocone positioned in the central part of the tooth or very slightly further back. The p4 with 2–3 relatively high supplementary cusps; rear presence of P3 and/or of p1/2. The first lower molar is only slightly constricted in the area between the trigonid and the talonid; its entoconid has 1–3 cusps in close proximity to each other, their size increases in a backward direction. The mandibular corpus is very deep; the coronoid process of the mandible is vertical.

D e s c r i p t i o n o f t h e B u l g a r i a n b e a r m a t e r i a l f r o m M i s h i n K a m i k . The MK bone sample exhibits an impressive robustness. All the skulls are from very old individuals, the teeth extremely worn, and canines absent. The skulls are robust and very wide, with massive zygomatic arches (Tab. 1); with a strongly domed



Text-fig. 1. Restoration of living appearance of *U. sa. rossicus* based on the fossil material from Mishin Kamik cave. Drawing by Assen Ignatov.

and bilobated frontal portion, especially in males (Text-fig. 1); the temporal crests are prominent and the sagittal crest is deep. In most cases the sagittal crest (as in many other cave bears) seems longitudinally split (or double) because of the not fully fused temporal lines on its dorsal surface from which the crest is formed (Pl. 1, Figs 1–3). The choanae are narrow, the muzzle is rather short, the palate is concave in the area of M2; the nasal aperture is oblique in lateral view; the rostral end of the nasal bones is at the level of the mesial

surface of P4. The glabella of the MK specimens is deep – varying from 7.85 to 15.4 mm (11.41 mean).

Two of the skulls (Nos. FM 3111, FM 3385) have a less domed (more oblique) frontal profile, practically without bilobation; frontals with weaker zygomatic processes and respectively a slightly narrower frontal width; weaker sagittal and transversal crests and less pronounced postorbital constriction. One of them (No. FM 3111) is the smallest of all the skulls from this location (Pl. 1, Fig. 3). We consider these two skulls to be from females.

The tooth morphology remains rather unclear due to the degree of wear. Nevertheless, when considering the P4 outlines it is possible to state that the protocone is placed relatively centrally, close to the paracone-metacone border and that the paracone and metacone are in line and not at an angle with respect to each other (Pl. 2, Fig. 6); these features could also be observed in some better preserved isolated teeth. Only one isolated M1 has a preserved occlusal morphology (Pl. 2, Fig. 7). It is archaic, with a limited number of swellings and cusplets, the middle longitudinal valley is narrow, wider only on the talonid. The mesocone is single; the cingulum is developed on the labial side from the protocone to the distal end of the hypocone. Two M2 have a preserved occlusal surface. Each of them has different morphology – one with a more complex morphology and with well-developed cingulum, the other with more simple morphology and without a cingulum (Pl. 2, Figs 8, 9). The hemi-mandibles are well preserved in the MK sample (Pl. 2, Figs 1–5, Tab. 2). Only one hemi-mandible has an alveolus

Table 1. Measurements of the cave bear skulls from Mishin Kamik. 1. Total length; 2. Condylarbasal length; 3. Basal length; 4. Neurocranium length; 5. Viscerocranum length; 6. Length of rostrum; 7. Palatal length; 8. Tooth-row length C1 to M2; 9. Tooth-row length P4 to M2; 10. Zygomatic width; 11. Neurocranium width; 12. Minimal skull width (postorbital width); 13. Interorbital width; 14. Condylar width; 15. Mastoid width; 16. Minimal palatal width; 17. Greatest palatal width; 18. Width of rostrum (at canines); 19. Greatest diameter of orbit; 20. Cranial height.

| | FM 3111 | FM 3112 | FM 3113 | FM 3114 | FM 3115 | FM 3385 | FM 3386 |
|----|---------|---------|---------|---------|---------|---------|---------|
| 1 | 344 | 355 | 363.5 | 375 | 394 | 365 | 370 |
| 2 | – | 337 | – | – | 374.3 | 350 | 357 |
| 3 | – | 319 | – | – | 354 | ~330 | 338 |
| 4 | 187.5 | 188.6 | 200.5 | 199.4 | 221 | 196 | 201 |
| 5 | 179.2 | 194.8 | 187.7 | 196 | 210.2 | 197.5 | 202 |
| 6 | 136.4 | 138.4 | 133 | 138 | 146.6 | 146 | 144 |
| 7 | 175.5 | 185.4 | – | 201 | 195 | 194 | – |
| 8 | 141 | 143.7 | 138 | 151.5 | 143.8 | 141 | 144.5 |
| 9 | ~86 | 82.5 | 80.9 | 86.4 | 82 | ~78 | 85 |
| 10 | 217 | 232 | 231.8 | ~254 | 263 | 241 | ~243 |
| 11 | 102.3 | 101.4 | 108.3 | 110.7 | 117.7 | 113 | 105 |
| 12 | 68.2 | 69 | 72.5 | 75.5 | 76.8 | 72 | 68 |
| 13 | 74.4 | 90 | 80 | 84.3 | 91.4 | 81.5 | 75 |
| 14 | – | 53 | – | – | 80 | – | 64.4 |
| 15 | 149.3 | – | – | – | 201.5 | ~165 | 178 |
| 16 | 33.8 | 38.1 | 45.3 | 47.7 | 44.5 | 46 | 42 |
| 17 | ~93 | 94.5 | 95.5 | 105.7 | 99 | ~100 | 103.3 |
| 18 | ~81.5 | ~90 | – | ~92 | ~99 | ~95 | 79 |
| 19 | 45.6 | 43 | 50 | 53 | 62.2 | 45 | 53 |
| 20 | – | 114.5 | – | – | 126.5 | – | 116 |

Table 2. Measurements of the cave bear hemi-mandibles from Mishin Kamik. 21. Mandibular length; 22. Mandibular length to the processus angularis; 23. Lower tooth row length (c1 – m3); 24. Lower cheek tooth row length (p4 – m3); 25. Height at ramus mandibularis; 26. Height behind m1; 27. Height at the diastema.

| | 21 | 22 | 23 | 24 | 25 | 26 | 27 |
|---------|-------|-------|--------|--------|--------|-------|--------|
| FM 3110 | – | – | 174 | 92.54 | – | 67 | 59.5 |
| FM 3334 | 294 | 290 | 178.5 | 94.8 | 134.8 | 70.8 | 63.4 |
| FM 3337 | 283.4 | 275.6 | 177.5 | 97.37 | ~128 | 61.3 | 59 |
| FM 3335 | ~276 | ~258 | 173 | 92.23 | 122.3 | 61.6 | 62 |
| FM 3338 | – | – | 177.4 | 101.13 | – | 65.6 | 62 |
| FM 3339 | 255 | 250.5 | ~161 | 90.66 | 116.14 | 54.6 | ~49 |
| FM 3330 | – | – | – | 90.65 | – | ~63 | 56 |
| FM 3341 | 240 | 234 | 147.16 | 82.89 | 113.7 | 60.09 | ~50.47 |
| FM 3336 | 246 | 237 | 152.54 | 90.43 | 115.24 | 60.9 | 56.09 |
| FM 3333 | 262.5 | 255 | 152.48 | 92 | – | 58.04 | 55.68 |
| FM 3332 | 282 | 278 | 173 | 92 | – | 63.18 | 58.53 |
| FM 3340 | – | – | ~154 | 87.22 | – | | 49.55 |
| FM 3331 | 279.5 | – | 171.5 | – | – | 67.31 | 57.93 |
| FM 3343 | – | – | 158 | 90.61 | – | – | 52.28 |

for p2; another has molars only (FM 3331; Pl. 2, Fig. 3), p4 is not developed at all, and this must be an anomaly. Some of the hemi-mandibles have a preserved p4 and it is possible to observe its morphology (Pl. 2, Figs 11a–15b). All of the specimens have a paraconid and metaconid more or less of a similar size, situated close to each other. In some cases, there is an additional cuspid of the same size behind them, and all p4 have smaller additional cuspets (morphotypes D2, D2/D3 after Rabeder 1989, Rabeder and Tsoukala 1990). The rather simple m1 morphology is without constriction between the talonid and the trigonid and with relatively more archaic entoconid (Pl. 2, Fig. 10). On the mandibles the preserved m1 are excessively worn, but in all cases the archaic outline is clearly visible. For all teeth measurements see Table 3.

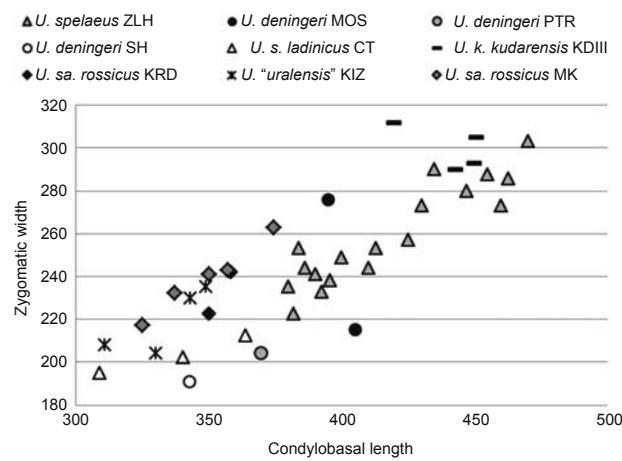
The postcranials are also robust (Pl. 4, Figs 1–9, Tabs 4–8). The lateral epicondyle of the humerus is enlarged, the lateral condyle of the femur distally protruding, the distal segments of the limbs (ulna, radius and especially the tibia) very shortened. The postcranials of males and females could be distinguished because of the different sizes.

Comparison of the Bulgarian bear material from Mishin Kamik

Compared to *Ursus arctos*, the MK bear differs in the robustness of the skull, by the completely different proportions, by the strongly domed frontals, the massive zygomatic arches and the better developed temporal crests, the larger muzzle with very wide surface for the incisors, much deeper palatal bone; visibly narrower choanae, the more complex cheek teeth morphology, absence of upper and lower anterior premolars (they very rarely persist, and are reduced in size). The nasal aperture is more oblique in lateral view and the nasal bones are more caudally situated: their rostral end is at the level of the mesial surface of P4 (in *U. arctos* it is normally at the level between I3 and C1). The postcranial elements are also more robust, the distal segments of the limbs are significantly shortened.

The noted features, as well as the extremely speleoid morphology of p4 (see Wagner and Čermák 2012) separate the bears from Mishin Kamik from the arctoid lineage and place them in the cave bear lineage.

The tooth morphology demonstrates a number of archaic features (see description). In this respect the Mishin Kamik bear is more similar to *U. deningeri* than to the large and more evolved cave bears from the *U. spelaeus-U. ingressus* group. This similarity is expressed also by the more or less similar size (length) of the skulls of some *U. deningeri* populations (SH and PTR for example) (Text-figs 2–4); the mean glabella depth is similar to that of *U. deningeri* from SH and PTR (García et al. 2007, Santos et. al. 2014). A comparison with *U. deningeri suessenbornensis* (considered by some authors, especially in older works, as a separate species) is practically impossible, as the type material is extremely scarce (see Baryshnikov 2007).

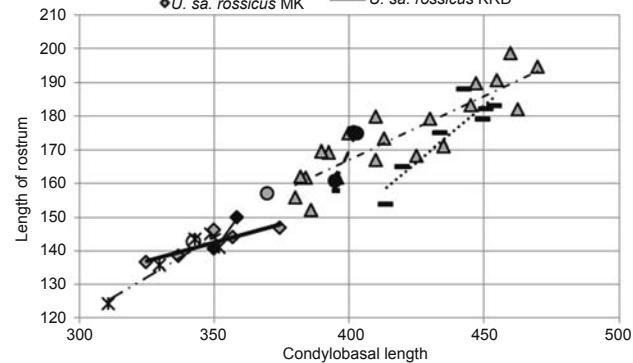


Text-fig. 2. Scatter diagram: condyllobasal length vs. zygomatic width in skulls of different cave bear taxa. Data after Rabeder et al. 2004, Baryshnikov 2007, Santos et al. 2014.

Table 3. Measurements of the cheek teeth of Mishin Kamik cave bears.

| Tooth | Specimen № | Maximal length | Maximal width |
|-------|------------|----------------|---------------|
| P4 | FM 3112 | 18.3 | ~13.4 |
| | FM 3113 | 18 | ~12.7 |
| | FM 3114 | 17.6 | ~13.4 |
| M1 | FM 3112 | 26.8 | 18.4 |
| | FM 3113 | 27.4 | ~18.08 |
| | FM 3115 | 24.5 | 13.7 |
| | FM 3388 | 25.46 | 17.93 |
| M2 | FM 3312 | 41.4 | 19.6 |
| | FM 3114 | 46 | 20 |
| | FM 3115 | 41.6 | 21 |
| | FM 3375 | 40.29 | 20.56 |
| | FM 3390 | 41.74 | 19.48 |
| | FM 3387 | 41.85 | 21.23 |
| p4 | FM 3330 | 15.26 | 9.59 |
| | FM 3334 | 15.54 | 9.98 |
| | FM 3336 | 14.98 | 9.81 |
| | FM 3333 | 15.15 | 9.82 |
| | FM 3343 | 14.9 | 9.33 |
| m1 | FM 3337 | 26.8 | 14 |
| | FM 3334 | 27.3 | 15.5 |
| | FM 3335 | 26.8 | 14 |
| | FM 3333 | 26.09 | 13.8 |
| | FM 3376 | 30.4 | 14.82 |
| m2 | FM 3334 | 28.8 | 19.8 |
| | FM 3335 | 27.5 | 17.6 |
| | FM 3339 | 25.7 | 16.2 |
| | FM 3331 | 30.54 | 19.15 |
| m3 | FM 3334 | 24.6 | 19.2 |
| | FM 3335 | 21.8 | 19.6 |
| | FM 3338 | 29.7 | 19.7 |
| | FM 3339 | 23.6 | 17.5 |

▲ *U. spelaeus* ZLH - *U. k. praekudarensis* KDI Regression line
 ● *U. deningeri* PTR - *U. k. kudarensis* KDIII - - - *U. spelaeus* ZLH - - - *U. "uralensis"* KIZ
 ● *U. deningeri* MOS ✕ *U. "uralensis"* KIZ - - - *U. deningeri* MOS - *U. sa. rossicus* MK
 ○ *U. deningeri* SH ♦ *U. sa. rossicus* KRD *U. k. kudarensis* KDIII
 ◊ *U. sa. rossicus* MK — *U. sa. rossicus* KRD



Text-fig. 3. Scatter diagram: condylobasal length vs. length of rostrum in skulls of different cave bear taxa. Data after Baryshnikov 2007, Santos et al. 2014.

Table 4. Measurements of cave bear humeri from Mishin Kamik. 1. Longest length (from caput humeri to the most distal point of the trochlea); 2. Depth of the caput humeri; 3. Proximal depth 4. Width of caput humeri; 5. Width of the diaphysis; 6. Greatest distal width.

| | FM 3104 | FM 3103 | FM 3389 | FM 3344 |
|---|---------|---------|---------|---------|
| 1 | 342 | 368 | 374 | 329 |
| 2 | 75.8 | 76.81 | 79 | - |
| 3 | 89.06 | - | 85 | - |
| 4 | 72 | 70.5 | 73.6 | - |
| 5 | 40.81 | 38.5 | 47 | 40.24 |
| 6 | 106.63 | 116.52 | 117.8 | 100.8 |

Table 5. Measurements of cave bear ulnae from Mishin Kamik. 1. Longest length; 2. Greatest depth of the olecranon; 3. Greatest width of the olecranon; 4. Depth at the diaphysis; 5. Greatest width at the coronoid process; 6. Distal depth.

| | FM 3354 | FM 3350 | FM 3351 |
|---|---------|---------|---------|
| 1 | 268.3 | ~290 | 289.5 |
| 2 | 57.4 | 70.6 | 69.3 |
| 3 | 36 | 46.6 | - |
| 4 | 31.2 | 27.2 | 33.3 |
| 5 | ~44 | 56.7 | ~56 |
| 6 | 37 | 46 | 45.4 |

Table 6. Measurements of cave bear radii from Mishin Kamik. 1. Longest length; 2. Greatest width at the proximal end; 3. Greatest depth at the proximal end; 4. Depth at the diaphysis; 5. Distal width; 6. Distal depth.

| | FM 3347 | FM 3357 | FM 3346 |
|---|---------|---------|---------|
| 1 | - | - | 280 |
| 2 | 44.45 | - | 50.56 |
| 3 | 34.8 | - | - |
| 4 | - | 28.6 | 31.6 |
| 5 | - | 56.4 | ~70 |
| 6 | - | ~31.8 | 43.84 |

On the other hand the skull shape and proportions differs from *U. deningeri* s. str. from the early Middle Pleistocene. In general, *U. deningeri* has a less wide (with some exceptions) skull (Text-fig. 2). The MK bear has abruptly and strongly elevated frontals and demonstrates the evolved profile of the *U. spelaeus-U. ingleseus* group: The stepped forehead forms a well developed dome, with a slight depression on the parasagittal line. The CT scan comparison (Pl. 3) revealed several specific profile peculiarities of the Mishin Kamik skulls (Pl. 3, Figs 3, 4), the features and the intraspecific variability in the development of the frontal sinuses as well as the thickness of the skull bones. The sinuses are large, they significantly extend backward and may occupy more than half of the brain cavity to about 2/3 of its length (Pl. 3, Figs 3, 4). The occipital region in the area of the external occipital

Table 7. Measurements of cave bear femora from Mishin Kamik. 1. Longest length from caput femoria; 2. Greatest depth at the caput femoria; 3. Greatest width at the proximal end; 4. smallest width at the diaphysis; 5. Greatest width at the distal end.

| | FM 3367 | FM 3358 | FM 3361 | FM 3359 | FM 3364 | FM 3360 | FM 3362 |
|---|---------|---------|---------|---------|---------|---------|---------|
| 1 | — | 374 | 336 | 372 | 398 | 378 | 325 |
| 2 | 47 | 51.6 | 45.6 | 53.6 | ~54 | 56.7 | 44.67 |
| 3 | 94.7 | 101.3 | 94.6 | 110.7 | 111.5 | 114.5 | 95.29 |
| 4 | 35 | 36.5 | 37.5 | 40.8 | 40.4 | 42.2 | 34.54 |
| 5 | — | — | 84.2 | 87.3 | — | 91.8 | 80.7 |

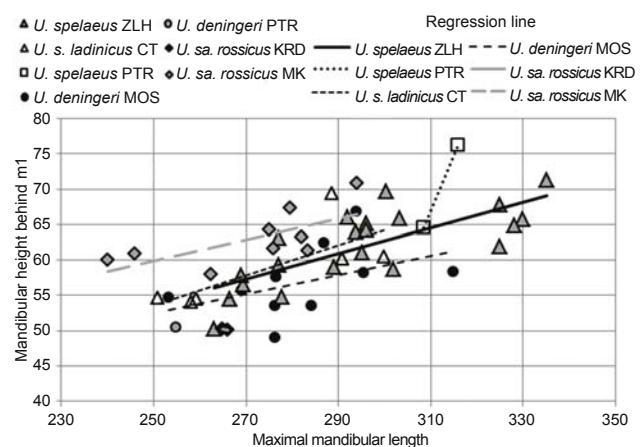
protuberance is very thick. In this respect the MK skulls show similarity with the scanned specimens of *U. spelaeus* from Spain (García et al. 2006, 2007, Santos et al. 2014) (Pl. 3, Figs 1, 2). The basioccipital is also thick (7.6 mm and 8.1 mm respectively) and most probably pneumatized as in *U. spelaeus*. In spite of its clearly smaller size, in width the MK skulls may measure the same or even exceed the relative width of the skulls of the *U. spelaeus-ingressus* gr. On the other hand their tooth morphology is less evolved (see description).

Comparison with *U. spelaeus ladinicus* Rabeder et al., 2004

The skull of this small, high alpine cave bear *U. s. ladinicus* or *U. ladinicus* from Conturines cave, is similar in skull size (Rabeder et al. 2004) to the MK bears. But all other proportions are clearly different: the zygomatic width is much larger in the MK sample, while the cheek teeth length is shorter (Text-figs 2, 4) and the mandibles are deeper (Text-fig. 5).

Comparison with *Ursus deningeroides* Mottl, 1964 and other taxa from large cave bear group

This bear from the Repolust cave in Austria was described by Mottl (1964) as a very primitive and small *U. spelaeus*. The locality is from the late Middle Pleistocene, with an estimated age of about 200 ka (ca. 223 ka for the lowermost level) (Döppes and Rosendahl 2009). The skulls are considerably larger and relatively narrower than in the MK bears (Text-fig. 6a). They are however as significantly

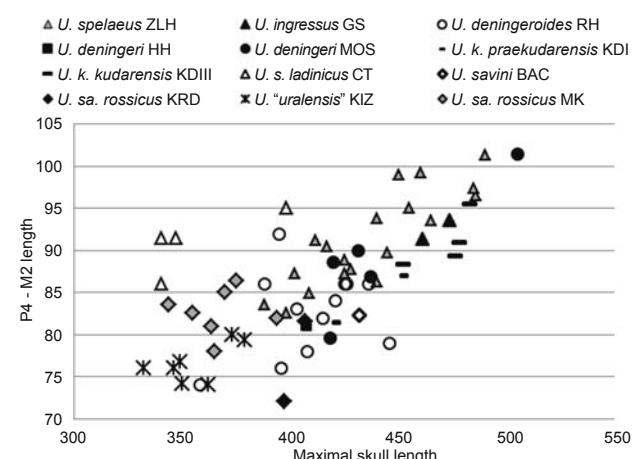


Text-fig. 5. Scatter diagram: maximal mandibular length vs. height behind m1 in different cave bear taxa. Data after Rabeder et al. 2004, Baryshnikov 2007, Baryshnikov and Tsoukala 2010.

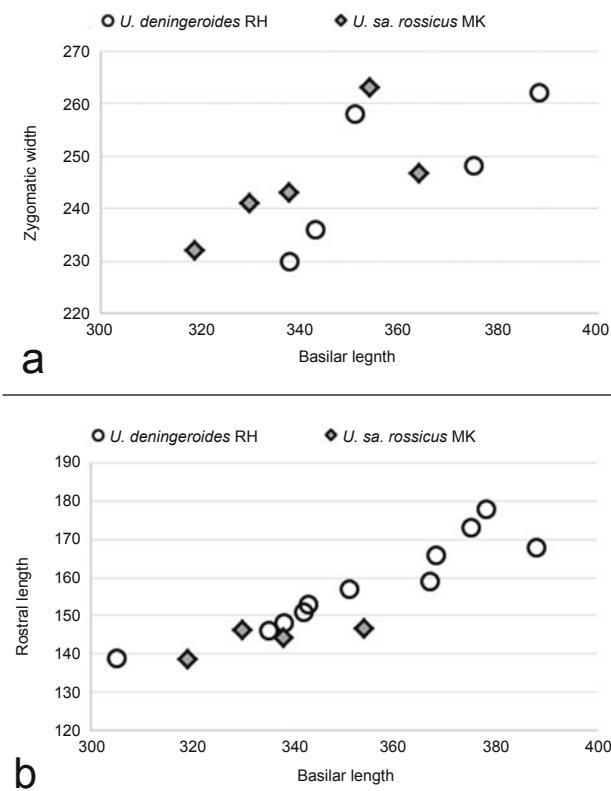
domed as in MK, but with a clearly slanting caudally neurocranial profile (see Mottl 1964: pl. 2, fig. 1 and pl. 3, fig. 1). The muzzles are longer in general (Text-fig. 6b). About 60% of specimens retain anterior premolars (P3/p3 and P1–2/p1–2) and m1 is to some degree more archaic than in MK. The mandible length of the Repolust cave bears are between 245–313 mm, and the depth under p4 varies from 50–71 mm. The MK mandibles are shorter (with maximal value 294 mm), while the depth under p4 varies from 54.29–71.7 mm, indicating a greater depth. The mandible depth between m2 and m3 is also greater in MK – 64–78 versus 50–75 mm for the Repolust cave bears.

A cave bear of small size is described from Einhornhöhle (Middle Pleistocene, Germany). There are only mandibles, no skulls are preserved (Schütt 1968); the p4 and m1 morphology is similar to that in the MK sample. The main difference in m1 morphology is the more complex metaconid and more acute paraconid in MK (sensu Grandal d'Angle and López-González 2004). The MK mandibles (with maximal length from 240 to 294 mm and mean value 269 mm) are smaller on the whole in relation to the Einhornhöhle specimens (260–319 mm, mean 280 mm). At the same time they are deeper: the depth under p4 varies from 54.29 to 71.7 mm (mean 62.8 mm) for MK and for the Einhornhöhle bears from 46 to 75 mm (mean 58 mm).

A small cave bear (*Ursus spelaeus parvitalipedis* TORRES, 1991) was described from the Late Pleistocene of Troskaeta cave, Spain (Torres et al. 1991). The mean value for the maximal mandibular length is 280.9 mm vs. mean



Text-fig. 4. Scatter diagram: maximal skull length vs. P4 – M2 length in skulls of different cave bear taxa. Data after Zapfe 1948, Rabeder et al. 2004, Baryshnikov 2007, Pacher (pers. comm. in 2017).



Text-fig. 6. Scatter diagrams: a) basilar length vs. zygomatic width in skulls of *U. deningeroides* RH and *U. sa. rossicus* MK. b) basilar length vs. rostral length in skulls of *U. deningeroides* RH and *U. sa. rossicus* MK. Data after Mottl 1964 and personal observations.

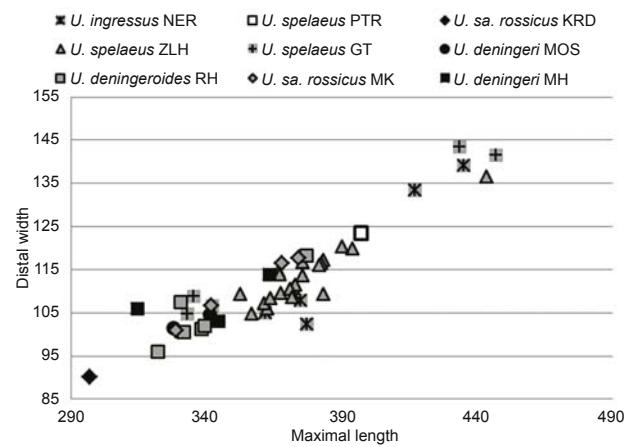
value of the height behind m1 – 65.2 mm. These mean values are similar in size to the MK bears (267 mm vs. 63 mm respectively), but more data are necessary for a reliable comparison and conclusions.

In comparison with *Ursus kudarensis praekudarensis* (BARYSHNIKOV, 1998) from the Middle Pleistocene of the Southern Caucasus (Baryshnikov 1998), the skulls from MK are smaller (Text-figs 3, 4), but their teeth morphology is more complicated; in *U. d. praekudarensis* p4 are narrower and more archaic; the m1 is also more archaic.

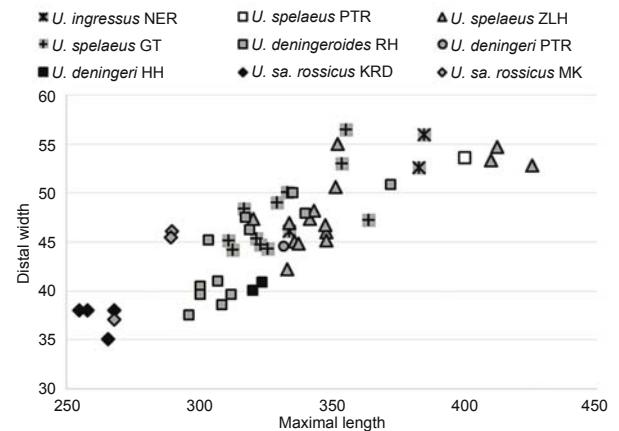
Ursus kudarensis kudarensis BARYSHNIKOV, 1985 from the Late Pleistocene (see Baryshnikov 1998) exhibit significantly larger skulls than those in the MK sample (Text-figs 1–3), but the teeth (P4, p4, m1) have a number of similarities (protocone on P4 is placed more mesially; developed paraconid and metaconids on p4, see in Kudaro III, layer 3–4; in m1, the junction between the trigonid and talonid is equal or slightly wider than the width of the trigonid, the metaconid is separated on two or more denticles, the entoconid consists of two or three cusps). Some DNA investigations put this bear phylogenetically somewhat apart from the clades of *U. deningeri* VON REICHENAU, 1904 and *U. ingressus-U. spelaeus* (see Knapp et al. 2009, Dabney et al. 2013).

Comparison with *Ursus rossicus* BORISSIAK, 1930

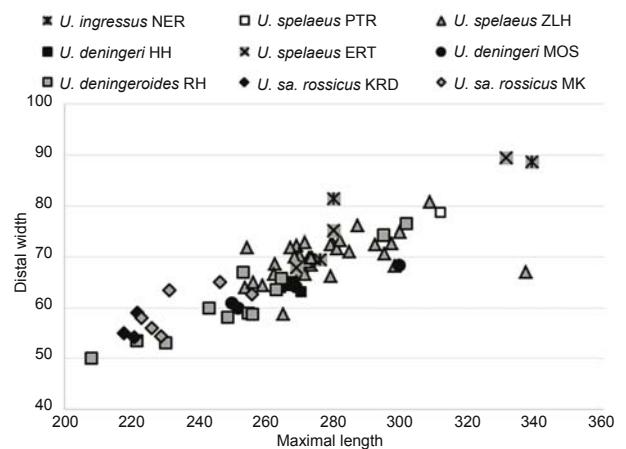
The bear from MK is very similar to *Ursus rossicus* (*U. sa. rossicus*) from the type locality, Krasnodar (Borissiak 1930, 1932), with a probable age at the very end of the



Text-fig. 7. Scatter diagram: maximal length vs. distal width of humeri in different cave bear taxa. Data after Borissiak 1932, Nagel et al. 2005, Athen 2007, Baryshnikov and Tsoukala 2010.



Text-fig. 8. Scatter diagram: maximal length vs. distal width of ulnae in different cave bear taxa. Data after Borissiak 1932, Nagel et al. 2005, Athen 2007, Baryshnikov and Tsoukala 2010.



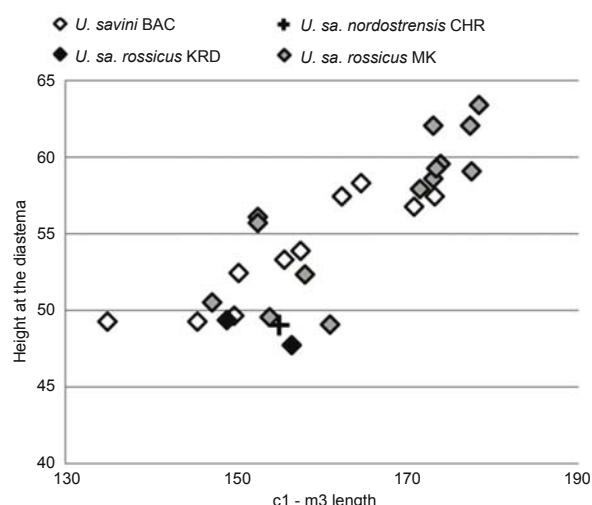
Text-fig. 9. Scatter diagram: maximal length vs. distal width of tibiae in different cave bear taxa. Data after Borissiak 1932, Nagel et al. 2005, Athen 2007, Baryshnikov and Tsoukala 2010.

Middle Pleistocene or the Eemian (Baryshnikov 2007). The skulls from Krasnodar are robust, clearly domed (Borissiak

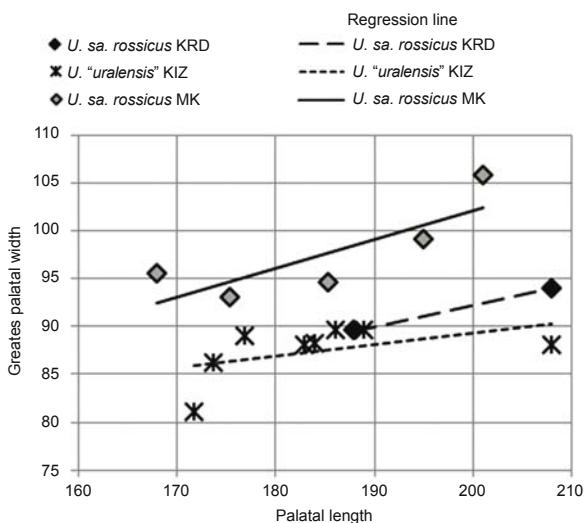
1932, Baryshnikov 2007) and similar to the MK bear in proportions. Their zygomatic width is large, similar to the sample from MK (Text-fig. 2). On P4 the protocone is in a central position between the labial cusps, but the tooth is to some extent more evolved than in *U. deningeri*, as it also seems to be in the MK sample. The lower teeth morphology are also similar: p4 has a well-developed paraconid and metaconid, and many additional cuspets; m1 is archaic with a very weak constriction only at the middle part. The postcranials are smaller, about the size of the female specimens from MK (Text-figs 8–10). Some small differences could however be seen: the upper cheek teeth row is shorter (Text-fig. 3). The mandibles have a slightly shorter depth than in the MK sample but the sample of *U. sa. rossicus* is very limited in number (Text-fig. 6).

Comparison with *U. savini* ANDREWS, 1922 from Bacton

Wagner and Čermák (2012) include in *U. savini* only the specimens from Bacton s. str. (Forest Bed locality). The exact provenance of the only known skull is unclear. The size and proportions of the MK sample compared to the Bacton mandibular material are very similar (Text-fig. 10), while some differences exist in the tooth morphology. In the MK sample the p4 morphology is more evolved to some extent, with a well-developed metaconid and paraconid and with many additional cuspets and swellings; m1 is similar in morphology, but with a better developed enthyoconid (sensu Rabeder 1999) and with more cuspets on the talonid. The only known skull from Bacton is a larger size (maximal length is 432 mm) and has a relatively short cheek teeth row in relation to its size, but the absolute length of the cheek teeth row (length of 82.3 mm) (M. Pacher, pers. comm. in 2017) is comparable to that in the specimens from MK. It is difficult to say without more data if this skull belongs to a different species (*U. deningeri* (?)) or to *U. savini* from the type locality. It is noteworthy, however, that the specimen had a short muzzle (considering the photo kindly sent by A. Stewart) and strongly domed frontals, which is not



Text-fig. 10. Scatter diagram: c1 – m3 length vs. height of mandibles in front of p4 in different cave bear taxa. Data after Baryshnikov 2007, Sher et al. 2011.



Text-fig. 11. Comparative skull proportions of the bear from Mishin Kamik, *U. sa. rossicus* from Krasnodar, and “*U. uralensis*” from Kizel cave. Data after Baryshnikov 2007.

typical for *U. deningeri*, especially at such an early stage in evolution of this species.

Comparison with *U. “rossicus” uralensis* VERESHCHAGIN, 1973 from Kizel cave

The small bear from Kizel cave (Ural, Russia) has several significant similarities in skull size and proportions to the MK bear, as well as to the typical *U. sa. rossicus* from Krasnodar (Text-figs 2, 3; see also: Vereshchagin and Baryshnikov 2000, Baryshnikov 2007). The metric comparison (Text-fig. 11; for comparison see also the photos in Vereshchagin 1973: fig. 9) shows however, that *U. sa. rossicus* has a wider skull, and in particular the muzzle, and that in this respect *U. uralensis* is similar to some extend, in our opinion, to the large cave bears of the *U. spelaeus-kanivetz/ingressus* group. The bear from Kizel is rather young in geologic age (around 40 000 B.P.). After several opinions it seems to be genetically related more or less to *U. ingressus* (Pacher et al. 2009, Stiller et al. 2014), but new palaeogenomic data are in contradiction with this view (Barlow 2017).

Discussion and conclusion

The MK bear sample has a unique combination of features. On one hand, it is more similar to *U. deningeri* (and/or to several of its forms/subspecies) in its size and in some primitive tooth features. On the other hand however, the skull morphology (the shape of the frontals, the expanded frontal sinuses, the neurocranial bone thickness – see above) is more advanced and p4/P4 also demonstrate some more advanced features with which the MK sample show several affinities with the *U. spelaeus-ingressus* group. It seems that the Mishin Kamik bear achieved the advanced skull features at a relatively old geological age in comparison to the “classic” large cave bears. With these characteristics and small size but marked cranial and mandibular robustness, the bears from Mishin Kamik differ from the *U. deningeri*

lineage as well as from the *U. spelaeus-ingressus* gr. The latter, more evolved group could represent, judging from the very similar morphology of *U. spelaeus* and *U. ingressus* (Baryshnikov 2007, Knapp et al. 2009, Ivanova et al. 2016), eastern and western branches of a mega-species in an early stage of speciation; i.e. *U. spelaeus* and *U. ingressus* must be considered as two semispecies following the terminology of Dobzhansky and Mayr (see Mayr 1969). (The second semispecies should be named *U. kanivetz* as Baryshnikov and Puzachenko (2017) mentioned that the name *Ursus kanivetz* VERESHCHAGIN, 1973 should have priority over *U. ingressus* RABEDER et al., 2004, and that this species may have two subspecies: *U. k. kanivetz* – Urals and *U. k. ingressus* – E. and Central Europe.)

The Mishin Kamik bear shares its specific characteristics with *U. sa. rossicus* from the loess of Krasnodar (see Borissiak 1930, 1932, Baryshnikov 2007) and both samples (KRD and MK) must represent one and the same taxon. Both samples may have a very similar geological age related to the very end of the Middle Pleistocene or the beginning of the Eemian. The mandibles from both Krasnodar and Mishin Kamik are very similar in size, proportions (markedly robust for their small size) and tooth-morphology and bear a resemblance to the sample from Bacton, described as *Ursus savini* (Andrews 1922). The p4 and m1 from Bacton demonstrates slightly less evolved features but this could be explained by the considerably older geological age (early Middle Pleistocene) of the BAC sample. We consider, with some caution, the only known skull from Bacton to be *U. savini* (see above). Two hypotheses are possible in relation to the affinities of the bear from BAC compared with the KRD-MK form: *U. sa. rossicus* (KRD and MK) is a separate, younger species, or all three samples represent one and the same form of small and robust cave bear. Again with caution, due to the lack of verified dated cranial material from BAC, we prefer to accept the second, simpler hypothesis, thereby supporting the statement of Baryshnikov (2007). Thus, we unify all the three samples in *U. savini*, considering the *U. sa. rossicus* form (KRD and MK) as a younger and more advanced subspecies. Wagner and Čermák (2012) summarized three hypotheses regarding the possible phylogenetic and taxonomic status of *U. savini*: 1) *U. savini* is an ancestor of *U. deningeri*; 2) *U. savini* is synonymous with *U. deningeri*; 3) *U. savini* is a representative of an independent lineage of small spelaeoid bears, representing the sister clade to the main *U. deningeri*-*U. spelaeus* lineage. Our data and analysis give us reason to accept the third suggestion.

Individual teeth from the Middle Pleistocene of Mala Balanica cave, Serbia (Cvetković and Dimitrijević 2014) show similarities in the simple morphology and size to the bears from MK and KRD and could represent a late form of *U. savini*.

Kurtén (1969) followed by Kahlke (1999) noted that the short-muzzled “*U. deningeri hundsheimensis*” ZAPFE, 1948 (which is considered to be among the typical representatives of *U. deningeri*) is very similar to *U. savini* due to its small skull size. It should also be mentioned in support of the above statement that “*U. deningeri hundsheimensis*” exhibits relatively bulging frontals (see Zapfe 1948: pl. 1), more expanded than is usual in *U. deningeri* and this

evolved stage of frontal shape was achieved by a very old population. The affinities of *U. savini* and “*U. deningeri hundsheimensis*” (with skull parameters which are rather similar to those of the KRD sample: Text-fig. 4) merit more detailed study.

The samples of *U. savini* from BAC, KRD and MK have similarities also with some small cave bears from the steppe regions of the early Middle to the Late (?) Pleistocene of Southern Siberia (Baryshnikov and Foronova 2001), but we prefer not to comment in detail on this similarity until the collection of more accurate data is available, especially regarding the age of the finds. The very small mandible with rather wide age determination (1.5–0.5 Ma) from the far North-East Siberian locality of Cherskiy, described as a new taxon *U. s. nordostensis* BARYSHNIKOV, 2011, seems indeed to show several similarities with *U. savini* (see Sher et al. 2011), especially in the size and proportions of the mandible corpus (Text-fig. 10), as well as in the structure of p4 and m1, which are similar to that of MK and KRD. Thus, it is possible to suggest that *U. savini* has an Asian-Siberian origin. At the same time we agree with Wagner and Čermák (2012) that not all small cave bears could have a common origin, and that the decrease in size could be related in a number of cases to a parallelism caused by an independent process of diminution within the cave bear lineage. Such are the cases at least in *U. spelaeus eremus*, *U. s. ladinicus* and *U. “rossicus” uralensis*. The ancient DNA data (Pacher et al. 2009, Stiller et al. 2014) show similarities between *U. uralensis* VERESHCHAGIN, 1973 (= *U. “rossicus” uralensis*) from Kizel cave (N. Urals), *U. kanivetz* VERESHCHAGIN, 1973 (also N. Urals) and *U. ingressus* from E. Europe. On the basis of this result (as well as some differences from *U. sa. rossicus* from M. Kamik, see above) we could suggest that “*U. uralensis*” represents a dwarf form retaining some plesiomorphic dental condition of the *kanivetz* group (sensu Baryshnikov and Puzachenko 2017), overall it is very similar to the latter clade. In general it would be difficult to imagine that the specialized skull morphology of *U. savini rossicus* could evolve into that of the *U. kanivetz-ingressus* clade, and so, we would not consider that the Kizel bear which is genetically similar to *U. ingressus* s. str., could be associated with the *U. savini* (*U. sa. rossicus* including) taxon.

According to the data from Bacton hills, the Krasnodar loess deposits and the fossil fauna and geology of the Mishin Kamik foothills’ area, the habitats used by *U. savini* (named also the “steppe cave bear” in Baryshnikov 2007, Sher et al. 2011) were related to mosaic landscapes in hilly but not mountain terrain. The late *U. savini* (according to the data from MK) was well adapted to grazing, much better than *U. arctos* and not worse than the *U. spelaeus-ingressus* gr. Evidence for this can be seen in the wide incisive arch and the caudally deep nasal aperture, which indicates the significant development of a food-catching upper lip. At the same time the choanae are narrow (in comparison with the brown bear), which in addition to the short distal segments of the limbs (especially the tibia) is an indication (Vereshchagin 1973) that this bear was not well adapted to running. But possibly it was well adapted to moving in hilly, rugged terrain. Some authors consider that the domed forehead of cave bears could be a result of the need for a large area for muscle attachment in relation to the mastication, leading to anisometric growth

of this skull region (Grandal-d'Anglade 2010). To this we should add, however, the probable relationship of the domed frontals with the development of the frontal sinuses, which may also be related to the development of the sense of smell (Spassov and Geraads 2015) necessary for distinguishing between the different foods in a vegetal/omnivorous diet.

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Explanations of the plates

PLATE 1

Mishin Kamik bear – skulls

1. Skull, FM 3113; a: lateral view, b: ventral view.
2. Skull, FM 3115; a: lateral view, b: ventral view.
3. Skull, FM 3111; a: lateral view, b: ventral view.

Scale bar = 100 mm.

PLATE 2

Mishin Kamik bear – mandibles and teeth

1. Hemi-mandible dex., FM 3332; lateral view.
2. Hemi-mandible dex., FM 3110; lateral view.
3. Hemi-mandible dex., FM 3331; lateral view.
4. Hemi-mandible dex., FM 3334; lateral view.
5. Hemi-mandible dex., FM 3335; lateral view.
6. P4 sin. with P3 alveolus from skull FM3113; occlusal view.
7. M1 dex., FM 3388; a: occlusal view; b: buccal view.
8. M2 dex., FM 3387; occlusal view.
9. M2 dex., FM 3375; occlusal view.
10. m1 sin., FM 3376; a: occlusal view, b: lingual view.
11. p4 sin. from mandible FM 3336; a: occlusal view, b: lingual view.
12. p4 sin. from hemi-mandible FM 3343; a: occlusal view, b: lingual view.
13. p4 dex. from hemi-mandible FM 3330; a: occlusal view, b: lingual view.
14. p4 dex. from hemi-mandible FM 3334; a: occlusal view, b: lingual view.
15. p4 sin. from hemi-mandible FM 3333; a: occlusal view, b: lingual view.

Scale bar for figures 1 to 5 = 100 mm; figures 6 to 11 not to scale, reduced to the same overall length.

PLATE 3

Comparison of the internal morphology in sagittal sections of the skulls of selected taxa of spelaeoid bears. The vertical lines mark the anterior and posterior projections of the frontal sinuses

1. CT scan of skull of *U. spelaeus* 1.
2. CT scan of skull of *U. spelaeus* 2.
3. CT scan of skull of *U. sa. rossicus* FM 3113.
4. CT scan of skull of *U. sa. rossicus* FM 3115.
5. CT scan of skull of *U. deningeri* SH.
6. CT scan of skull of *U. deningeri* PTR.
7. Laser scan of skull FM 3113 (same as 3). The line on the frontals shows where the glabella depth has been taken.

1, 5 and 6 after Santos et al. 2014; 2 after García et al. 2007 (not to scale).

PLATE 4

Mishin Kamik bear – long bones

1. Humerus sin., FM 3389; cranial view.
2. Humerus sin., FM 3344; cranial view.
3. Ulna dex., FM 3351; lateral view.
4. Radius sin., FM 3346; cranial view.
5. Femur sin., FM 3359; caudal view.
6. Femur sin., FM 3360; caudal view.
7. Femur dex., FM 3361; caudal view.
8. Tibia dex., FM 3384; cranial view.
9. Tibia sin., FM 3383; cranial view.

Scale bar = 10 cm.

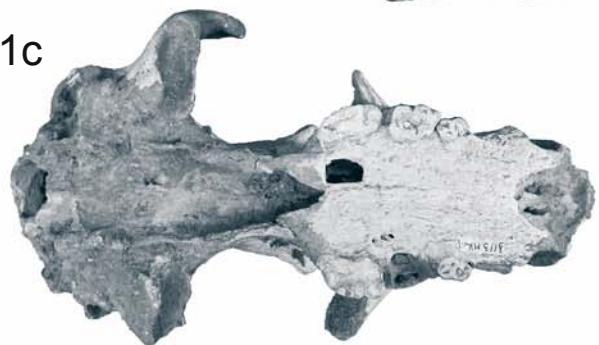
PLATE 1



1a



1b



1c



2a



2b



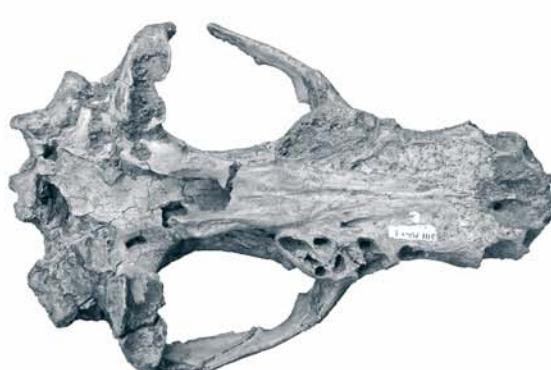
2c



3a



3b



3c

PLATE 2

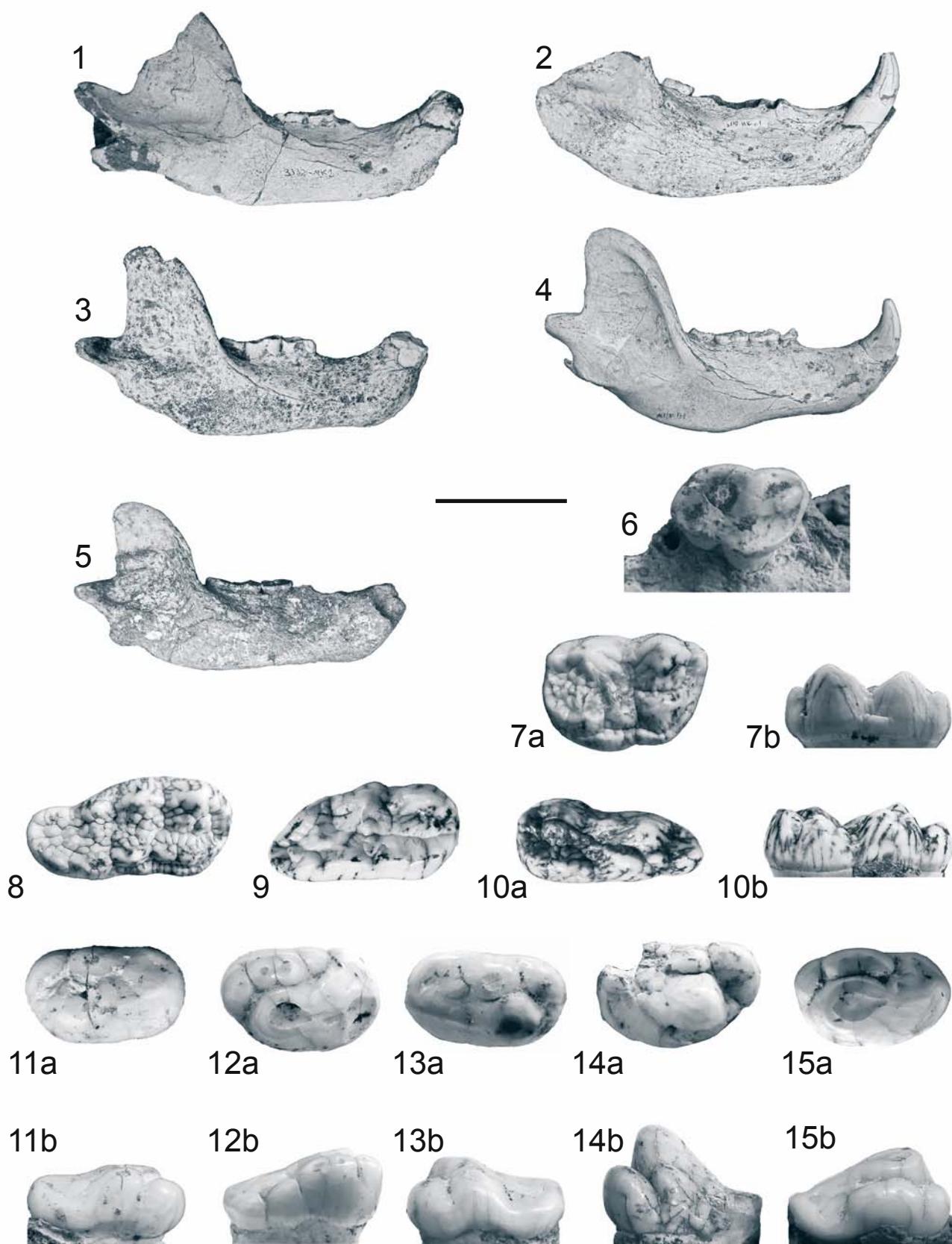


PLATE 3

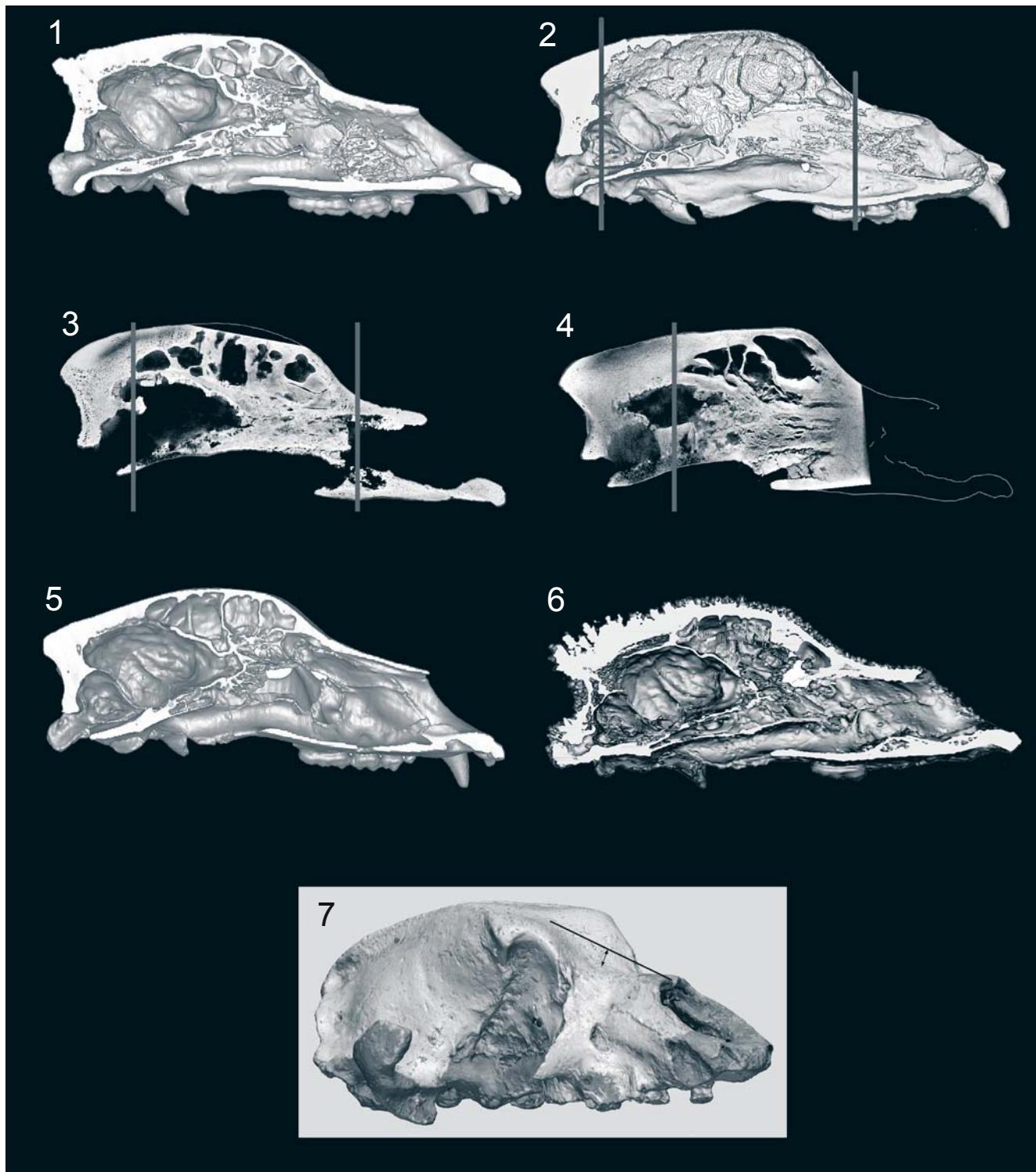


PLATE 4

