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Carnivores from the Borsuka Cave (southern Poland) as an example of changes in carnivore assemblages during MIS 2 and MIS 1

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Abstract. Two faunal assemblages were identified in the fossil material of carnivores from the Borsuka Cave. The older one, of Late Pleistocene age, found in layers V-VII and dated as the end of MIS 3 and MIS 2, included nine species: *Vulpes lagopus*, *Vulpes* sp., *Ursus arctos arctos*, *Gulo gulo*, *Meles meles*, *Martes martes*, *Mustela erminea*, *Mustela nivalis* and *Lynx lynx*. The younger assemblage, dated as MIS 1 and found in layers I-IV, comprised six species: *Vulpes vulpes*, *Ursus arctos arctos*, *Meles meles*, *Martes martes*, *Mustela* ex. gr. *eversmanni-putorius* and *Felis silvestris*. The carnivore material was represented by almost all skeletal elements, with the majority constituted by cranial bones, isolated teeth, vertebrae, metacarpals and metatarsals. Remains of *Vulpes vulpes* and *Meles meles* were the most abundant; the presence of young individuals of both species confirmed that they used the cave as a shelter and to raise cubs. The other carnivores were much rarer. Especially the occurrence of uncommon members of Late Pleistocene paleocommunities: *Gulo gulo* and *Lynx lynx* is noteworthy. Some components of the older assemblage: *Ursus arctos arctos* and *Gulo gulo*, represented large, robust forms, whose great size according to Bergman's rule was an adaptation to cool climate conditions. Likewise, the two smallest mustelids, *Mustela erminea* and *Mustela nivalis*, were represented by small and gracile specimens which were characteristic of Late Pleistocene cold phases. Metrically and morphologically the animals from the younger period dated as MIS 1 corresponded to the modern European forms.

Key words: Carnivora, morphology, Late Pleistocene, Holocene, faunal assemblage.

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I. INTRODUCTION

The Borsuka Cave (50°9'53''N 19°42'12''E) is located on the northern slope of the Szklarka valley in the southern part of Polish Jura, ca. 20 km west of Kraków (Fig. 1). The site was discovered in 2007, during cataloguing and exploration of the Szklarka valley caves (NOWAK 2007). Excavations were carried out in 2008-2010 and a single trench of 4x3 m was dug next to the cave entrance (WILCZYŃSKI et al. 2012a, 2012b).

Seven layers were distinguished in the profile: I – clay dump; the so-called “old heap”, II – black-dark brown humus, dated as 2.3 ka BP to 0.7-0.6 ka AD, III – red-dark brown clays with admixture of weathered siliceous fragments dated as 4.2-3.8 ka BP, IV – grey-yellow colluvial loess dated as 8.0-4.5 ka BP, V – pale-yellow, strongly compacted loess with admixture of siliceous, fine, sharp-edged rubble dated as 20.0-15.0 ka BP, VI – greyish-yellow clay mixed with sharp-edged unweathered limestone rubble dated as 27.0-25.0 ka BP, VII – dark brown clay situated in a rock crevice (Table I) (WILCZYŃSKI et al. 2012a, 2012b, 2016).

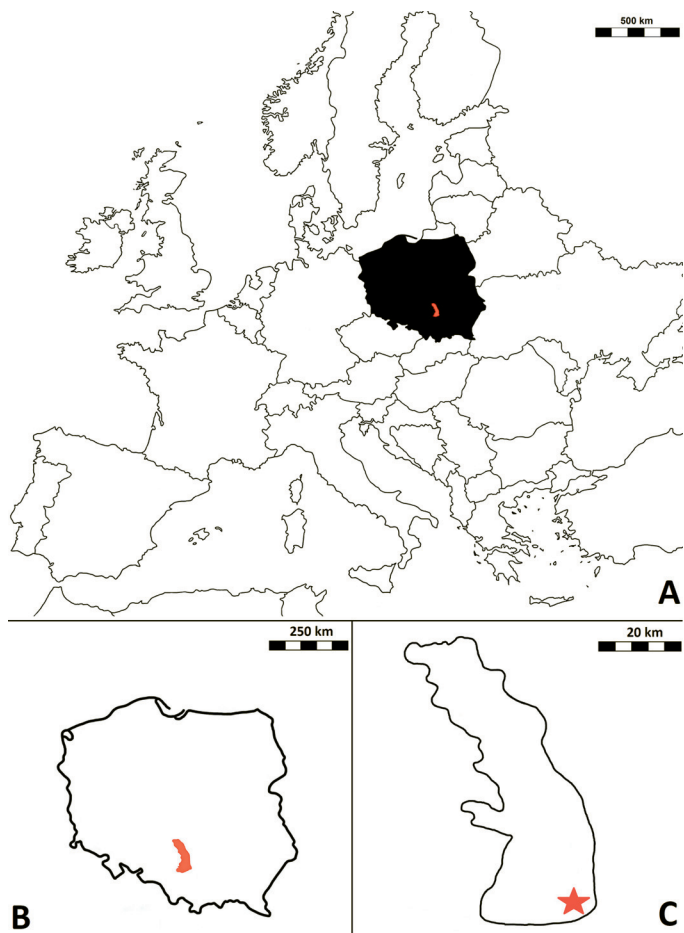


Fig. 1. Location of the Polish Jura in Europe (A) and in Poland (B), and location of the Borsuka Cave in the Polish Jura (C). Scale bars in km.

Table I

List of ^{14}C AMS dates obtained for specimens from the Borsuka Cave. The dates were calibrated with OxCal software (version OxCal v4.2.1 Bronk Ramsey, 2013). Atmospheric data from REIMER et al. (2009). The calibrated dates have 95.4% probability

Species	Bone	Layer	Lab. no	Uncal. date BP	Cal. date BP	Source
<i>Ursus arctos arctos</i>	ulna	III	Poz-93986	10380 \pm 60	10479 \pm 206	this work
<i>Felis silvestris</i>	mandible	III	Poz-27235	3920 \pm 35		WILCZYŃSKI et al. 2012a
<i>Meles meles</i>	humerus	III	Poz-27281	4175 \pm 35		WILCZYŃSKI et al. 2012a
<i>Mammuthus primigenius</i>	rib	speleologists trench	Poz-26124	24850 \pm 200	29851 \pm 327	NADACHOWSKI et al. 2011
<i>Alces alces</i>	incisor	VI	Poz-38236	25150 \pm 160		WILCZYŃSKI et al. 2016
<i>Bison priscus/Bos primigenius</i>	incisor	VI	Poz-32394	27350 \pm 450		WILCZYŃSKI et al. 2012a, 2016
<i>Rangifer tarandus</i>	metatarsus	VI	Poz-39237	26430 \pm 180		WILCZYŃSKI et al. 2012a, 2016

Overall, two faunal assemblages can be distinguished in Borsuka Cave. The older one, of Late Pleistocene age, found in layers V-VII was dated as the end of MIS 3 and MIS 2. The faunal list comprised *Columella columella*, *Pupilla loessica*, *Ena montana*, *Discus rotundatus*, *Vitrea crystalline*, *Aegopinella pura*, *Aegopinella* sp., *Nesovitrea hammonis*, *Oxychilus glaber*, *Zonitidae* spp., *Limacidae*, *Clausilia dubia*, *Clausiliidae* spp., *Perforatella incarnata*, *Perca fluviatilis*, *Lota lota*, *Coregonus* sp., *Cyprinidae* spp., *Rana temporaria*, *Bufo* sp., cf. *Anser* sp., *Accipiter gentilis*, *Lagopus muta*, *Tetrao tetrix*, *Tetrao urogallus*, *Lanius collurio*, *Sorex runtonensis*, *Sorex araneus*, *Neomys anomalus*, *Neomys fodiens*, *Talpa europaea*, *Cricetus cricetus*, *Dicrostonyx gulielmi*, *Lemmus lemmus*, *Clethrionomys glareolus*, *Arvicola terrestris*, *Microtus arvalis/agrestis*, *Microtus gregalis*, *Microtus oeconomus*, *Apodemus sylvaticus/flavicollis*, *Lepus* sp., *Ochotona pusilla*, *Vulpes lagopus*, *Vulpes* sp., *Ursus arctos*, *Gulo gulo*, *Meles meles*, *Martes martes*, *Mustela erminea*, *Mustela nivalis*, *Lynx lynx*, *Mammuthus primigenius*, *Equus ferus*, *Coelodonta antiquitatis*, *Rangifer tarandus*, *Alces alces*, *Bos primigenius/Bison priscus* and *Bos primigenius* (WILCZYŃSKI et al. 2012a, 2012b, 2016).

The younger assemblage, dated as the Holocene and found in layers I-IV included *Zonitidae* spp., *Limacidae* spp., *Clausiliidae* spp., *Helicidae* spp., *Rana temporaria*, *Bufo* sp., *Zamenis longissimus*, *Natrix natrix*, *Vipera berus*, *Anser albifrons*, *Anser anser* forma domestica, *Anser* sp., cf. *Anser* sp., *Anas platyrhynchos*, *Tetrao tetrix*, *Bonasa bonasia*, *Perdix perdix*, *Gallus gallus* forma domestica, *Galliformes* indet., *Crex crex*, *Scolopax rusticola*, *Columba* sp., *Strix aluco*, *Sorex araneus*, *Talpa europaea*, *Spermophilus superciliosus*, *Sciurus vulgaris*, *Castor fiber*, *Cricetus cricetus*, *Clethrionomys glareolus*, *Arvicola terrestris*, *Microtus subterraneus*, *Microtus arvalis/agrestis*, *Microtus oeconomus*,

Apodemus sylvaticus/flavicollis, *Mus musculus*, *Glis glis*, *Lepus* sp., *Oryctolagus cuniculus*, *Vulpes vulpes*, *Ursus arctos*, *Meles meles*, *Martes martes*, *Mustela* ex. gr. *eversmannii-putorius*, *Felis silvestris*, *Capreolus capreolus*, *Cervus elaphus*, *Capra/Ovis* and *Bos taurus* (WILCZYŃSKI et al. 2012a, 2012b, 2016).

II. METHODS AND MATERIAL

II.1. METHODS

Measurements were taken point to point, with an electronic calliper, to the nearest 0.01 mm. Each value given here is the mean of three measurements. Measurements shown in brackets denote the estimated value of the dimension. Additionally, some measurements were taken using a set for image analysis Olympus (Olympus stereo microscope ZSX 12, camera Olympus DP 71, programme Cell D). This set, coupled with camera Canon EOS 5D, was also used to take photographs. Osteological and dental terminology follows ANDERSON (1970). The measurements are shown in Figs 2-10.

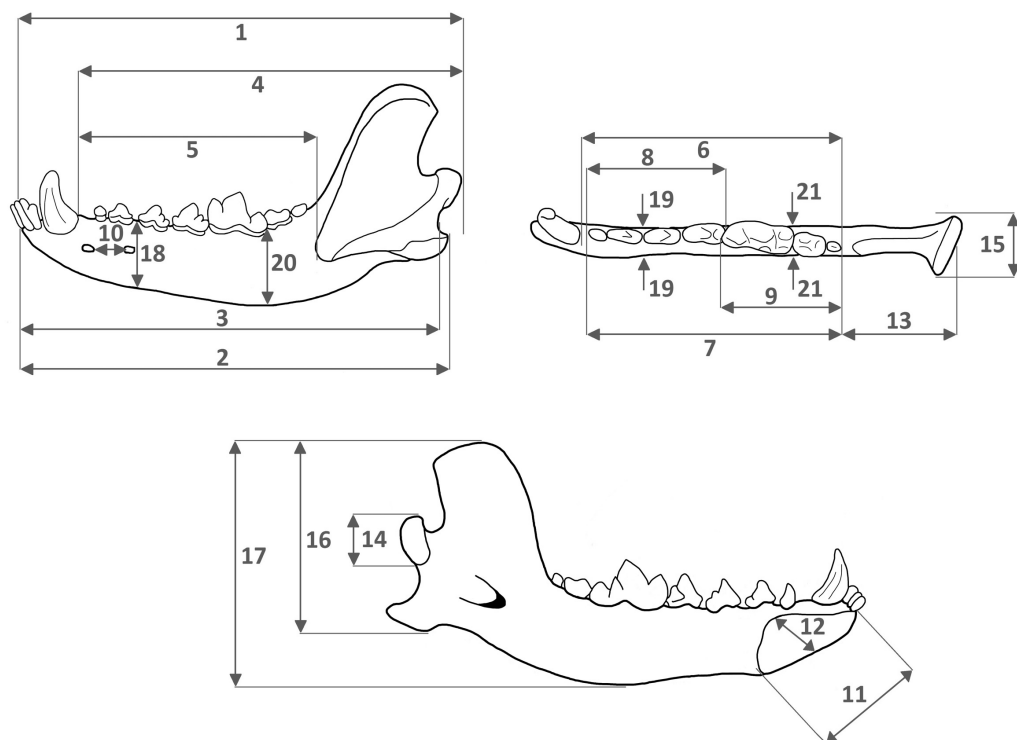


Fig. 2. Scheme of measurements of canid mandible: **1** – total length (infradentale to condyle), **2** – distance: infradentale to angular process, **3** – distance: infradentale to angular indentation, **4** – distance: behind c1 to condyle, **5** – infradentale to anterior margin of masseter fossa, **6** – posterior margin of c1 to posterior margin of m3, **7** – cheek teeth row length (anterior margin of p1 to posterior margin of m3), **8** – premolar row length (anterior margin of p1 to posterior margin of p4), **9** – molar row length (anterior margin of m1 to posterior margin of m3), **10** – distance between mental foramina, **11** – symphysis maximum diameter, **12** – symphysis minimum diameter, **13** – posterior margin of m3 to condyle length, **14** – condyle height, **15** – condyle breadth, **16** – angular process to coronoid process height, **17** – mandible maximum height, **18** – mandible body height between p2 and p3, **19** – mandible body thickness between p2 and p3, **20** – mandible body height between m1 and m2, **21** – mandible body thickness between m1 and m2.

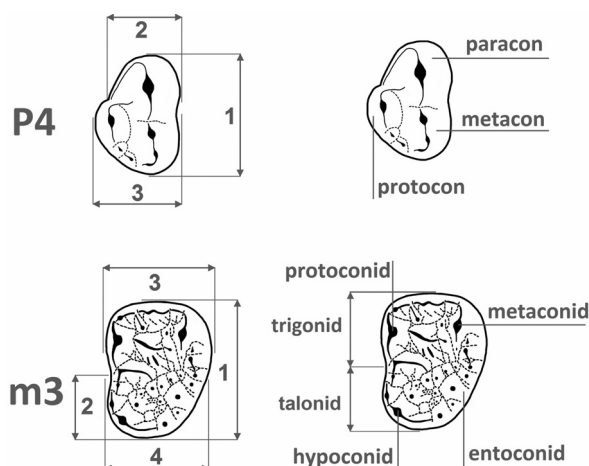


Fig. 3. Measurements (left) and cusp terminology (right) of ursid teeth P4 and m3. **P4:** 1 – total length, 2 – anterior breadth, 3 – posterior breadth; **m3:** 1 – total length, 2 – talonid length, 3 – trigonid breadth, 4 – talonid breadth.

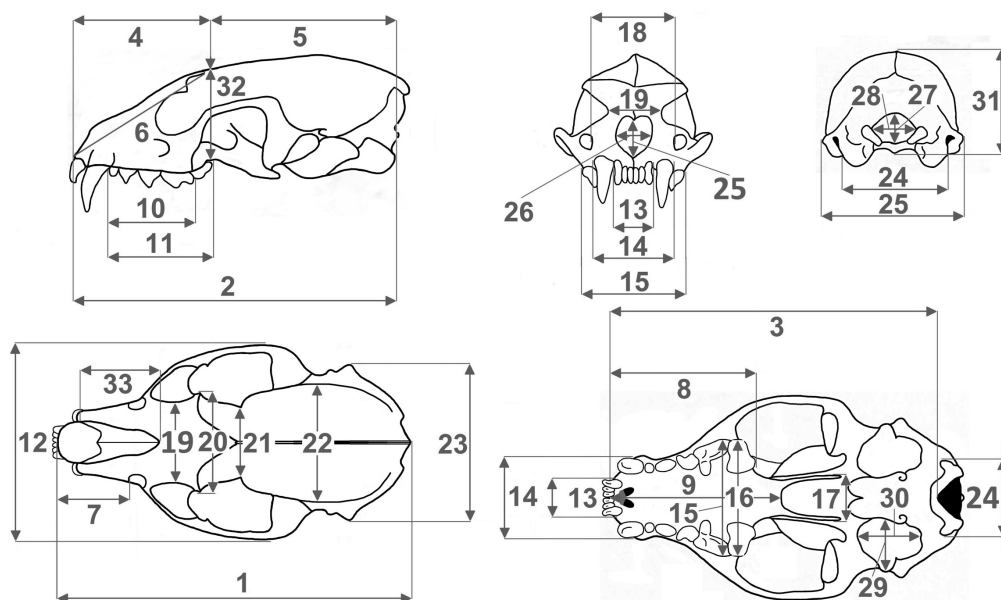


Fig. 4. Scheme of measurements of mustelid calvarium: 1 – total length (prosthion – acrocranium), 2 – condylo-basal length (prosthion – occipital condyles), 3 – basal length (prosthion – basion), 4 – viscerocranium length (prosthion – point F), 5 – neurocranium length (point F – acrocranium), 6 – facial length (prosthion – point F), 7 – rostrum length (prosthion – infraorbital), 8 – rostrum length (anterior margin of I1 to posterior margin of M1), 9 – palatal length (prosthion – staphylion), 10 – C1 – M1 length on alveoles (anterior margin of alveole of C1 to posterior margin of alveole of M1), 11 – upper premolar row length on alveoles (anterior margin of alveole of P2 to posterior margin of alveole of P4), 12 – breadth at zygomatic arches (zygion – zygion), 13 – incisor row breadth (I3 – I3 breadth), 14 – maximum breadth at canine alveoli, 15 – maximum breadth at P4 alveoli, 16 – maximum breadth at M1 alveoli, 17 – least palatal breadth, 18 – least distance between infraorbital foramina, 19 – least distance between orbits (entorbital – entorbital), 20 – frontal breadth (ectorbital – ectorbital), 21 – postorbital least breadth (postorbital bar), 22 – maximal neurocranium breadth (euryon – euryon), 23 – mastoid breadth (otion – otion), 24 – maximum breadth of occipital condyles, 25 – nasal aperture height, 26 – nasal aperture breadth, 27 – height of foramen magnum (basionopisthion), 28 – breadth of foramen magnum, 29 – bullae ossae length, 30 – bullae ossae breadth, 31 – cranial height (acrocranium – basion), 32 – maximum cranial height (staphylion – frontal).

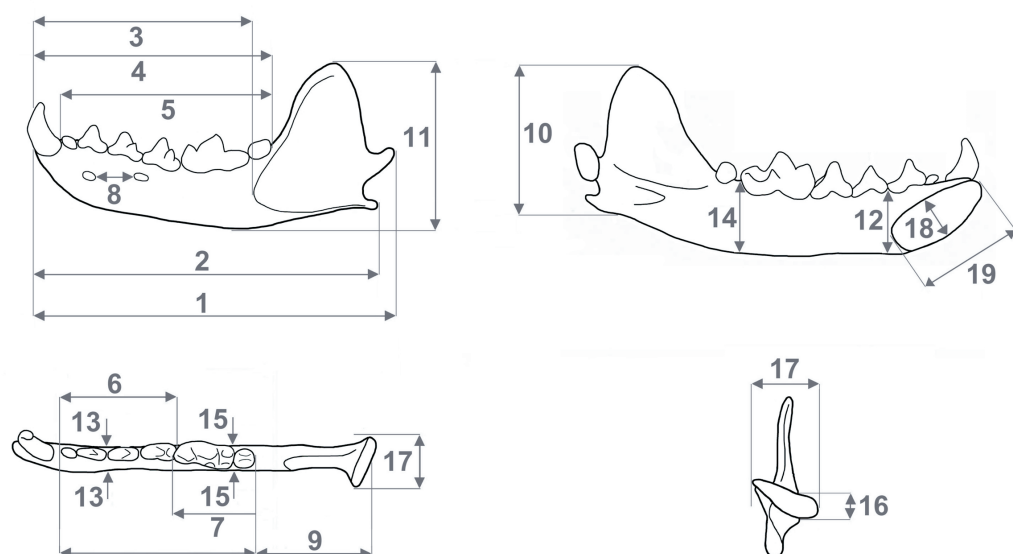


Fig. 5. Scheme of measurements of mustelid mandible: **1** – total length (condyle to infradentale), **2** – distance: angular process to infradentale, **3** – distance: infradentale to anterior margin of masseter fossa, **4** – distance: anterior margin of c1 to posterior margin of m2, **5** – cheek teeth row length (anterior margin of p1 to posterior margin of m2), **6** – premolar row length (anterior margin of p1 to posterior margin of p4), **7** – molar row length (anterior margin of m1 to posterior margin of m2), **8** – distance between mental foramina, **9** – distance: posterior margin of m2 to condyle, **10** – distance: angular process to coronoid process, **11** – mandible maximum height, **12** – mandible body height between p3 and p4, **13** – mandible body thickness between p3 and p4, **14** – mandible body height between m1 and m2, **15** – mandible body thickness between m1 and m2, **16** – condyle height, **17** – condyle breadth, **18** – symphysis maximum diameter, **19** – symphysis minimum diameter.

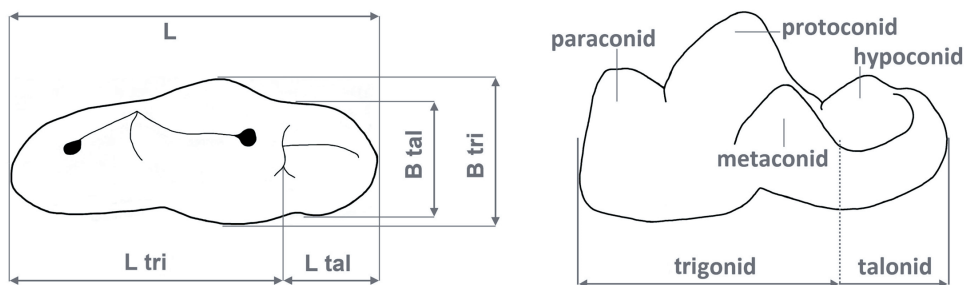


Fig. 6. Lower carnassial (m1) measurements (left) and cusp terminology (right): **L** – total length, **L tri** – trigonid length, **L tal** – talonid length, **B tri** – trigonid breadth, **B tal** – talonid breadth, tri – trigonid, tal – talonid, par – paraconid, pro – protoconid, met – metaconid, hyp – hypoconid.

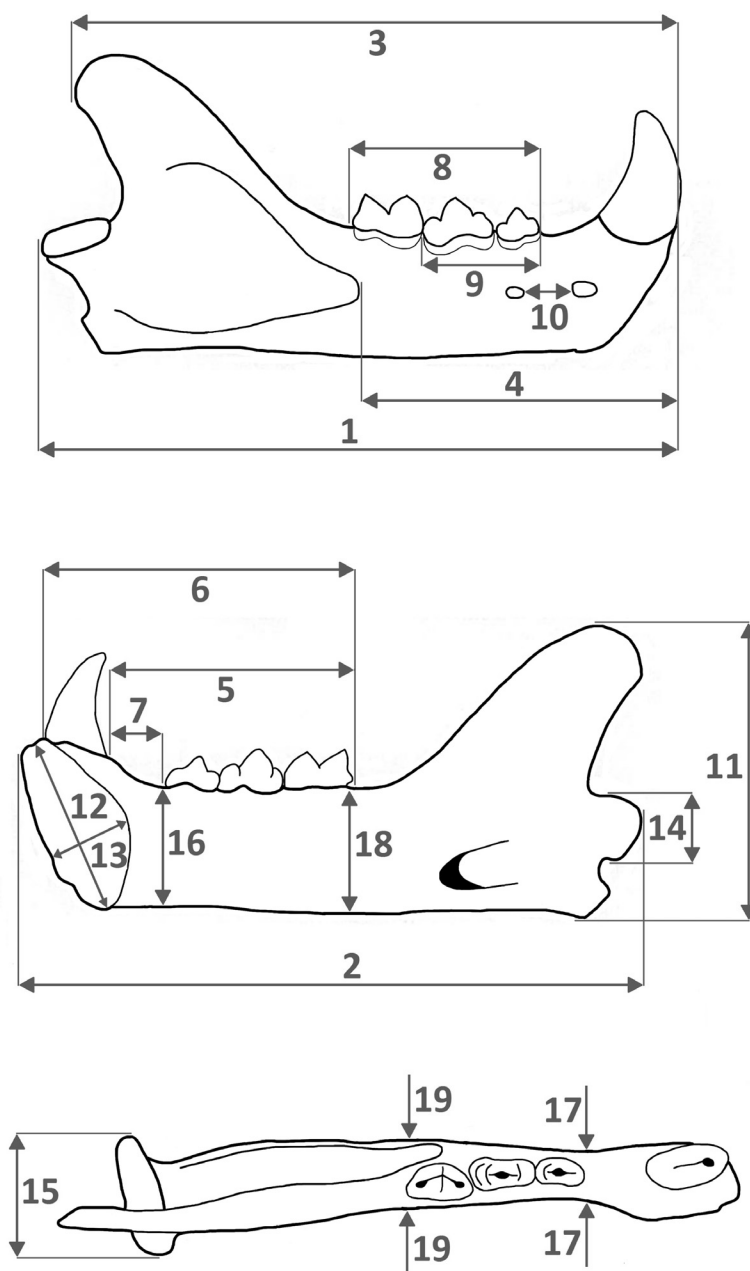


Fig. 7. Scheme of measurements of felid mandible: 1 – total length (infradentale to condyle), 2 – distance: infradentale to angular process, 3 – distance: infradentale to coronoid process, 4 – infradentale to anterior margin of masseter fossa, 5 – anterior margin of c1 to posterior margin of m1, 6 – posterior margin of c1 to posterior margin of m1, 7 – diastema length, 8 – cheek teeth row length (anterior margin of p3 to posterior margin of m1), 9 – premolar row length (anterior margin of p3 to posterior margin of p4), 10 – distance between mental foramina, 11 – angular process to coronoid process height, 12 – symphysis maximum diameter, 13 – symphysis minimum diameter, 14 – condyle height, 15 – condyle breadth, 16 – mandible body height before p3, 17 – mandible body thickness before p3, 18 – mandible body height behind m1, 19 – mandible body thickness behind m1.

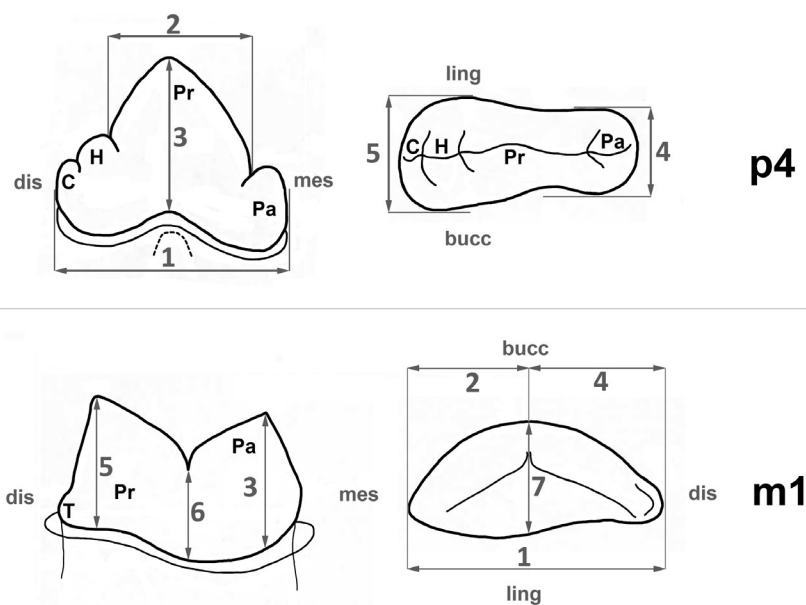


Fig. 8. Scheme of measurements of felid teeth: p3, p4 and m1. Left – lateral view, right – occlusal view, mes – mesial side, dist – distal side, ling – lingual side, bucc – buccal side, pa – paraconid, pr – protoconid, h – hypoconid, t – talonid, c – cingulum. **p3/p4:** 1 – total length, 2 – protoconid length, 3 – protoconid height, 4 – anterior breadth, 5 – posterior breadth. **m1:** 1 – total length, 2 – paraconid length, 3 – paraconid height, 4 – protoconid length, 5 – protoconid height, 6 – crown height, 7 – breadth.

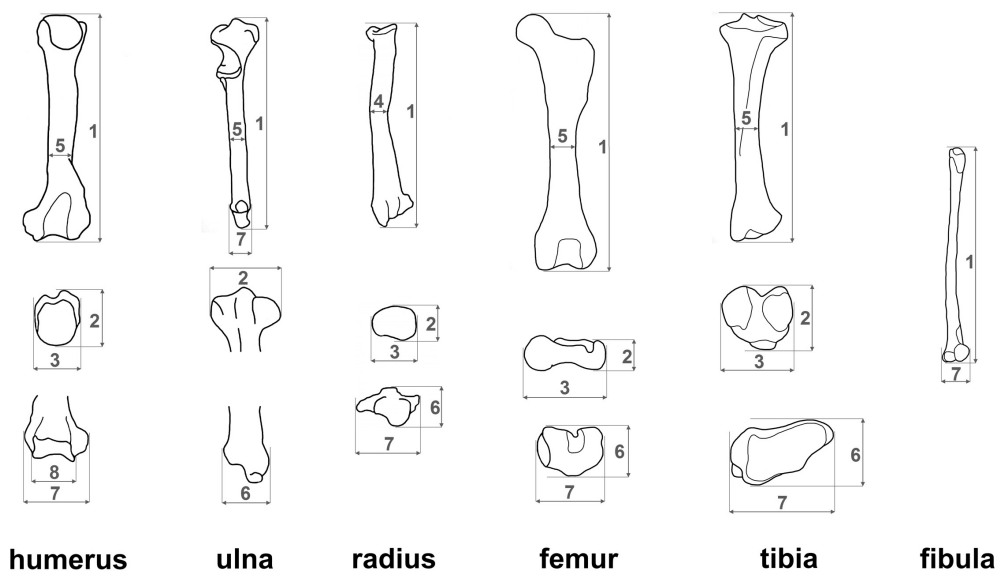


Fig. 9. Scheme of measurements of long bones: 1 – total length, 2 – proximal epiphysis depth, 3 – proximal epiphysis breadth, 4 – antero-posterior shaft length, 5 – minimum shaft breadth, 6 – distal epiphysis depth, 7 – distal epiphysis breadth, 8 – trochlear breadth.

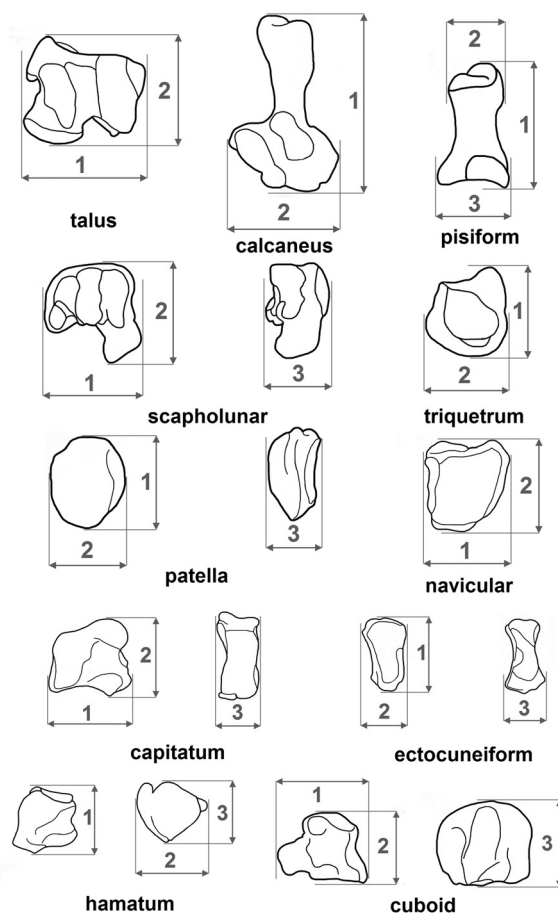


Fig. 10. Scheme of measurements of post-cranial bones: 1 – length, 2 – breadth, 3 – depth.

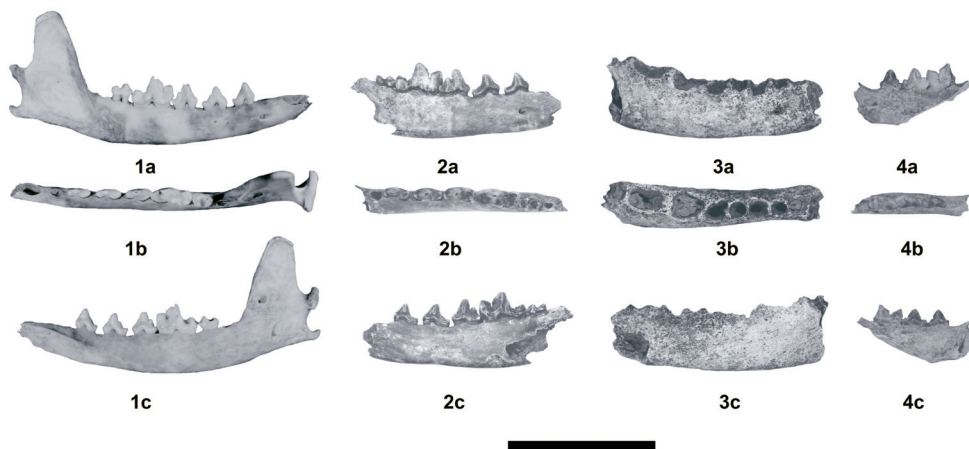


Fig. 11. Mandibles of medium-sized carnivores from the Borsuka Cave: right mandible of *Vulpes vulpes* MF/7065 (1a-c), left mandible of *Vulpes lagopus* MF/6982 (2a-c), right mandible of *Meles meles*; scale bar 20 mm.

II.2. MATERIAL

The material described here comes from the excavations conducted by the team leader Jarosław WILCZYŃSKI in 2008-2010 with cooperations of Michał WOJENKA from Institute of Archaeology, Jagiellonian University. The trench of 4x3 m was located near the cave entrance (WILCZYŃSKI et al. 2012a, 2016). All the material is stored at Institute of Systematics and Evolution of Animals, Polish Academy of Sciences in Kraków (Table II).

Table II

Inventory catalogue from the Borsuka Cave (symbol “–” – without the layer, usually heap)

Inv. no	Bone	Layer
<i>Canis lupus</i>		
MF/7069	left trapezium	VI
<i>Vulpes vulpes</i>		
MF/7070	right C1	–
MF/7072	left mandible body with deciduous m1	II
MF/7064	left mandible with damaged symphysis and present c1 and p2-m2	–
MF/7065	right mandible with p2-m2	–
MF/7066	left C1	–
MF/7067	right C1	–
MF/7068	right c1	–
MF/7110	left p2	VI
MF/7111	left m3	VI
MF/7052	left scapula	–
MF/7053	right scapula	–
MF/7009	right humerus	II
MF/7008	right ulna	II
MF/7006	left radius	II
MF/7007	right radius	II
MF/7055	left mtpc II	–
MF/7056	right mtpc II	–
MF/7071	left mtpc IV lacking distal end	II
MF/7057	left mtpc V	–
MF/7038	right navicular	–
MF/7013	proximal end of left femur	II
MF/7012	right femur	II
MF/7011	proximal epiphysis of left tibia	II
MF/7010	right tibia lacking distal end	II
MF/7051	fragment of left pelvis	–
MF/7107	left calcaneus	I
MF/7037	right cuboid	–
MF/7039	right patella	–
MF/7040	right ectocuneiform	–
MF/7041	right pisiform	–
MF/7073	left mtpc III	II

Inv. no	Bone	Layer
MF/7058	left mtts II	–
MF/7059	right mtts II	–
MF/7074	left mtts III without distal end	II
MF/7060	left mtts III without distal epiphysis	–
MF/7061	right mtts III	–
MF/7062	right mtts IV	–
MF/7063	left mtts V	–
MF/7054	distal end of mtpd	–
MF/7036	caudal	–
MF/7112	ph I lacking proximal end	II
MF/7042	manubrium of sternum	–
MF/7043	ph I	–
MF/7044	ph I	–
MF/7045	ph II	–
MF/7046	ph II	–
MF/7047	ph III	–
MF/7048	ph III	–
MF/7049	ph III	–
MF/7050	ph III	–
MF/7014	costae	–
MF/7015	costae	–
MF/7016	costae	–
MF/7017	costae	–
MF/7018	damaged costae	–
MF/7019	damaged costae	–
MF/7020	damaged costae	–
MF/7021	damaged costae	–
MF/7022	damaged costae	–
MF/7023	atlas	–
MF/7024	cervical	–
MF/7025	thoracic	–
MF/7026	thoracic	–
MF/7027	thoracic	–
MF/7028	lumbar	–
MF/7029	lumbar	–

Table II – cont.

Inv. no	Bone	Layer
MF/7030	lumbar	–
MF/7031	lumbar	–
MF/7032	lumbar	–
MF/7033	lumbar	–
MF/7034	lumbar	–
MF/7035	sacrum	–
MF/7075	caudal	III
<i>Vulpes lagopus</i>		
MF/6986	right I2	VI
MF/7005	left I3	VI
MF/6988	left C1	VII
MF/6991	left M1 crown	VI
MF/6992	anterior part of right M1 crown	VI
MF/6987	crown of right M2	VII
MF/7004	crown of left M2	VI
MF/7003	left i2	VI
MF/6993	left i3	VI
MF/6995	right i3	VI
MF/7001	left c1	VI
MF/7000	right c1	VI
MF/6998	left p2	VI
MF/7002	left p3	VI
MF/6994	left p4	VI
MF/6990	left m1	VI
MF/6999	left m2	VI
MF/6996	worn left p4	VI
MF/6983	fragment of left mandible body with m1	VI
MF/6982	right mandible body with p2-m2	VI
MF/6984	right patella	VI
MF/6997	right scapholunar	VI
MF/6985	ph I lacking proximal end	VI
<i>Vulpes sp.</i>		
MF/7094	left I2	VI
MF/7086	left I2	VI
MF/7102	left P1	VI
MF/7097	right P1	VI
MF/7098	right P1	VI
MF/7092	crown fr. of left P4	VI
MF/7083	fragment of left mandible body	VI
MF/7089	left i1	VI
MF/7096	left i2	VI
MF/7105	crown of right I2	VI
MF/7104	crown fragment of right c1	VI
MF/7093	left p1	VII
MF/7099	left p1	VI

Inv. no	Bone	Layer
MF/7106	right p1	VI
MF/7103	right p1	VI
MF/7095	right p1	VI
MF/7100	left p3	VI
MF/7101	posterior crown part of right p4	VI
MF/7090	right p3	VI
MF/7078	pm crown	II/III
MF/7087	damaged right scapholunar	VI
MF/7108	right mtcp III lacking distal end	III
MF/7109	shaft of left femur	I/III
MF/7077	right tibia lacking proximal end	I
MF/7076	right mts IV without distal end	III
MF/7084	mtpd without proximal end	VI
MF/7079	ph I	III
MF/7080	ph I	VI
MF/7091	ph I lacking distal end	VI
MF/7085	ph II lacking proximal end	VI
MF/7088	ph II	VI
MF/7081	ph III	VI
MF/7087	ph III	VI
<i>Ursus arctos arctos</i>		
MF/6981	left C1 fr.	III
MF/6977	right P4	III
MF/6979	left m3	VI
MF/6980	shaft fragment of right ulna	III
MF/6978	shaft fragment of left ulna	II/III
E6/68	shaft fragment of right ulna (destroyed to C14 date)	III
<i>Gulo gulo</i>		
MF/6976	right mts II without distal epiphysis	VI
<i>Meles meles</i>		
MF/6950	calvarium without zygomatic arches and with left P4-M1	II
MF/6906	right C1	III
MF/6917	right C1	VII
MF/6937	damaged ramus with fr. of left mandible body	II
MF/6942	right mandible body without symphyseal part	–
MF/6924	left i3	III
MF/6905	left c1	II
MF/6956	proximal end of left scapula	II/III
MF/6957	shaft fr. of left humerus	VI
MF/6932	left humerus lacking proximal end	III

Table II – cont.

Inv. no	Bone	Layer
MF/6944	damaged proximal epiphysis of left humerus	burrow
MF/6949	shaft fragment of right humerus	III
MF/6911	right humerus	III
MF/6935	shaft of right humerus	II
MF/6910	right humerus lacking proximal end	II
MF/6931	shaft fragment of left ulna	III
MF/6955	left ulna without distal end	–
MF/6940	shaft of right ulna	I
MF/6947	shaft of right ulna	I/ –
MF/6930	damaged proximal end of right ulna with shaft fr.	III
MF/6951	left radius lacking distal end	II/III
MF/6936	left radius shaft	II
MF/6920	right radius	III
MF/6926	right radius without proximal epiphysis	III
MF/6916	left mtcp I	VI
MF/6921	left mtcp II	III
MF/6934	left mtcp II	II
MF/6913	left mtcp III	III
MF/6922	left mtcp III	III
MF/6954	right mtcp III	III
MF/6909	left mtcp V	burrow
MF/6952	fragment of right pelvis	II/ –
MF/6939	left femur shaft	II
MF/6929	left femur without distal end	III
MF/6938	right femur shaft	II
MF/6943	left tibia shaft	II
MF/6945	damaged proximal end of left tibia	III
MF/6941	left tibia shaft	–
MF/6927	left tibia lacking proximal end	III
MF/6946	right tibia shaft	III
MF/6919	left fibula without distal end	III
MF/6914	right calcaneus	III
MF/6923	left mtts I	III
MF/6915	left mtts II	VI

Inv. no	Bone	Layer
MF/6933	left mtts III	II
MF/6912	left mtts III	III
MF/6907	right mtts IV	III
MF/6925	left mtts V	III
MF/6908	left mtts V	II
MF/6958	ph II	III
MF/6961	costa shaft fragment	III
MF/6960	costa shaft fragment	III
MF/6928	damaged atlas	III
MF/6959	damaged cervical	III
MF/6948	damaged lumbar	III
MF/6918	thoracic	III
MF/6953	caudal	II/ –
<i>Martes martes</i>		
MF/6969	worn, right c1	III
MF/6968	left p4	VI
MF/6967	posterior crown part of left p4	VI
<i>Mustela sp. (ex. gr. eversmanii-putorius)</i>		
MF/6970	mandible body right with deciduous p3-m1	III
MF/6971	left femur	–
<i>Mustela erminea</i>		
MF/6989	worn, left m1	VI
<i>Mustela nivalis</i>		
MF/6972	right P4	VI
MF/6973	right mandible body without symphysis and with p4-m2	VI
MF/6974	right mandible body without symphysis and with p4-m1	VI
<i>Lynx lynx</i>		
MF/6975	right ph I-1-a with damaged distal end	VI
<i>Felis silvestris</i>		
MF/6964	left mandible body without symphysis and with p3-m1	III
MF/6962	left c1	II
MF/6965	left c1	VI
MF/6963	left cuboid	III
MF/6966	left mtts III	–

III. TAXONOMIC PART

Twelve species from four carnivore families were found in the sediments of the Borsuka Cave: three canids, one bear, six mustelids and two felids (Table III). The most abundantly represented species were *Vulpes vulpes* and *Meles meles*, while remains of other species were scarce. However, even the most abundant species were represented only by

Table III

Carnivore assemblage from the Borsuka Cave

Species	NISP/MNI
<i>Canis lupus</i>	1/1
<i>Vulpes vulpes</i>	73/3
<i>Vulpes lagopus</i>	23/1
<i>Vulpes</i> sp.	33
<i>Ursus arctos arctos</i>	6/1
<i>Gulo gulo</i>	1/1
<i>Meles meles</i>	57/5
<i>Martes martes</i>	3/2
<i>Mustela</i> ex. gr. <i>eversmanii-putorius</i>	2/1
<i>Mustela erminea</i>	1/1
<i>Mustela nivalis</i>	3/2
<i>Lynx lynx</i>	1/1
<i>Felis silvestris</i>	5/1

few specimens, since large parts of skeletons of the red fox or badger were found. Also remains of *Vulpes lagopus*, including 24 bones, mainly isolated teeth, belonged in fact to one, at most two individuals.

Canis lupus LINNAEUS, 1758

An isolated post-cranial bone belonged to a large canid, of the size and proportions indistinguishable to those of the grey wolf. Although the individual is not small, much larger specimens are known from other sites, also in the Sudetes Mts, for example the Niedźwiedzia Cave. Unfortunately, no tooth remains which would permit distinction between the different forms of *C. lupus* were found, and the few skeletal remains are insufficiently diagnostic. For this reason, the large canid was classified as *C. lupus*.

Vulpes vulpes (LINNAEUS, 1758) and *Vulpes lagopus* LINNAEUS, 1758

Two small and morphologically very similar foxes were found in the sediments of the Borsuka Cave: the red fox *Vulpes vulpes* mostly in the Holocene period and the polar fox *Vulpes lagopus* in the Late Pleistocene sediments. Teeth of the red fox are on average slightly larger than those of the polar fox, however the size differences are not so significant (Tables IV-V). I3 of both species was larger than I1 and I2, with an elongated and curved crown. *V. vulpes* has a larger and stronger I3, with a more massive and curved crown. Also, the lingual cingulum is weaker developed. The upper canine is elongated and narrow, with an only slightly developed lingual cingulum. The canines of *V. lagopus* are smaller in size, shorter and less curved than those of *V. vulpes*. P4 of *V. lagopus* is on average smaller and more robust, with proportionally shorter protocon, which is less oriented mesio-lingually in the anterior direction (BARYSHNIKOV 2015).

The triangular M1 in *V. lagopus* has a well-developed metaconulus strongly connected with the posterior part of hypocon, the protoconulus is less developed and more closely associated with the protocon. The triple hypocon is large and smooth, while the mesial cingulum is rather weak. In the general occlusal view M1 of *V. lagopus* is narrower and smaller, with proportionally longer and narrower talon. The trigon is not so broad as in *V. vulpes*, with its main cusps lower and almost equal in size (RABEDER 1976).

The differences in M2 morphology between the two fox species are even more pronounced than in M1: the tooth in *V. lagopus* is much smaller, narrower and more reduced than in *V. vulpes*. The talon area is narrow and short, separated from the trigon by a deep, V-shaped valley. The metaconulus and the protoconulus are not connected, and both cusplets are more reduced (RABEDER 1976).

Table IV

Mandible and teeth dimensions of canids from the Borsuka Cave (mm). For measurements scheme of mandible see Fig. 2. Measurements of teeth according to VON DEN DRIESCH (1976)

Measurement		<i>Vulpes vulpes</i>		<i>Vulpes lagopus</i>
		MF/7064	MF/7065	MF/6982
Mandible	1		102.80	
	2		102.43	
	3		97.98	
	4	91.34	90.94	
	5	64.90	65.67	50.31
	6	62.98	62.20	55.04
	7	59.80	58.74	53.74
	8	36.03	35.54	30.86
	9	26.02	26.00	23.56
	10	12.42	10.81	
	11		28.14	
	12		8.53	9.56
	13	29.97	29.64	
	14	5.42	5.42	
	15	13.58	13.58	
	16	37.28	37.56	11.84
	17	43.27	41.45	5.74
	18	11.13	10.94	14.09
	19	5.88	5.71	5.82
	20	14.50	15.24	
	21	6.40	6.23	
c1	L	8.04		
	B	3.91		
p2	L	7.74	7.62	7.42
	B	3.09	3.04	3.12
p3	L	8.36	8.42	8.24
	B	3.19	3.17	3.39
p4	L	8.92	8.86	9.16
	B	3.96	3.97	4.18
m1	L	14.19	14.22	14.04
	L tri	9.87	9.84	9.74
	L tal	4.41	4.35	4.32
	B tri	5.52	5.58	5.23
	B tal	5.51	5.49	4.86
m2	L	7.08	7.04	6.28
	B	5.11	5.02	4.23

Table V

Measurements of isolated canid teeth from the Borsuka Cave (mm). Measurements of teeth according to VON DEN DRIESCH (1976)

Species	Coll. no	Tooth	L	B
<i>Vulpes vulpes</i>	MF/7070	C1	7.94	4.82
<i>Vulpes vulpes</i>	MF/7066	C1	6.61	3.78
<i>Vulpes vulpes</i>	MF/7067	C1	6.87	3.89
<i>Vulpes vulpes</i>	MF/7068	c1	7.18	3.79
<i>Vulpes vulpes</i>	MF/7110	p2	7.64	3.27
<i>Vulpes vulpes</i>	MF/7111	m3	2.99	2.37
<i>Vulpes lagopus</i>	MF/7003	i2	3.82	3.04
<i>Vulpes lagopus</i>	MF/6986	I2	4.23	3.35
<i>Vulpes lagopus</i>	MF/6995	i3	4.11	3.46
<i>Vulpes lagopus</i>	MF/6993	i3	3.86	3.65
<i>Vulpes lagopus</i>	MF/6988	C1	6.67	4.22
<i>Vulpes lagopus</i>	MF/7000	c1	8.06	4.33
<i>Vulpes lagopus</i>	MF/7001	c1	8.44	4.37
<i>Vulpes lagopus</i>	MF/6998	p2	7.61	3.14
<i>Vulpes lagopus</i>	MF/7002	p4	8.43	3.57
<i>Vulpes lagopus</i>	MF/6996	p4	9.19	4.31
<i>Vulpes lagopus</i>	MF/6991	M1	9.76	11.58
<i>Vulpes lagopus</i>	MF/6983	m1	13.74	5.38
<i>Vulpes lagopus</i>	MF/6990	m1	14.68	5.52
<i>Vulpes lagopus</i>	MF/7004	M2	4.59	7.39
<i>Vulpes lagopus</i>	MF/6987	M2	4.82	6.44

The mandible body of *V. lagopus* is shorter and more massive, with a more pronounced difference in massiveness between its anterior and posterior parts. Also, the curvature of the lower mandible margin, which starts at the p3/p4 border is more marked in *V. lagopus*. (Fig. 11). The lower teeth row is more curved in *V. lagopus* than in *V. vulpes*, and the diastemas between the back teeth p4, m1, m2, and m3 are shorter, and the teeth are closer together. Except for the smaller average dimensions, there are no reliable morphological differences between the lower incisors of the red and polar foxes. The lower canines of *V. lagopus* are metrically smaller than c1 of *V. vulpes*, with proportionally shorter and more curved crowns. The p1 alveola is more rounded in *V. lagopus*, while some differences in morphology of the premolars are discernible between both species. However, these imprecisely defined features have not been commonly applied in taxonomical analyses and their diagnostic value has not been widely discussed in the literature. Also, the great intraspecific variation of both species effectively hinders the correct taxonomical assignment. On average, the premolars in *V. lagopus* are more massive, their posterior part is slightly shorter, and the difference between the narrower anterior and the broader posterior parts is less marked. However, the differences between isolated teeth are so tentative and unreliable, that single premolars are usually classified as undetermined members of the genus *Vulpes* (RABEDER 1976).

The lower carnassial of *V. lagopus* differs considerably from m1 of *V. vulpes* in its more compact build, longer and broader trigonid, and a smaller metaconid, and a narrower and shorter talonid. The two largest cusplets in the talonid, the hypoconid and the entoconid, are lower and separated from one another by a deep and broad valley. In *V. vulpes* both cusplets are quite high and connected by a transverse, well-developed thick ridge. The number of additional small cusplets is usually smaller in *V. lagopus* than in *V. vulpes*. In *V. lagopus* m2 is smaller and more elongated than in *V. vulpes*. The crown is lower and in occlusal view more oval, with a narrower and proportionally longer talonid, a medium-sized hypoconid, a minute entoconid and no mesoconid (RABEDER 1976; BARYSHNIKOV 2015).

According to the methodology proposed by SZUMA (2004), based on the morphological variation of the talonid occlusal surface in m1 of *V. vulpes*, the two m1 from the Borsuka Cave represented the morphotype P4. It seems that overall the red fox dentition is highly conservative and shows negligible morphological changes through time (BARYSHNIKOV 2006). In foxes, males are somewhat larger than females. The vast number of red fox bones from the Borsuka Cave probably belonged to two individuals, however it is not excluded that a greater number of individuals was represented. The measurements indicate that the remains of *V. lagopus* belonged to a fully adult, medium-sized individual (Table III). It is impossible to say if it was a large female or a small male. The remains of *V. vulpes* belonged to a young, adult but rather small animal, with dimensions smaller than the values for the modern Polish red fox (Table IV). The most probable explanation is that they represented a fully grown but young red fox female.

Besides the mandibular material and the isolated teeth listed above, the material included also a variety of post-cranial bones (Figs 12-13): long bones and their fragments, numerous additional bones, metacarpals and metatarsals, and phalanges. Almost all of them were classified as *V. vulpes*, while only few post-cranial bones were assigned to *V. lagopus* (Figs 12-13). There are some morphological differences in the proportions of bones and muscle attachments, but they are not significant. On average the long bones, metacarpals, metatarsals and phalanges of *V. lagopus* are shorter and more gracile (Table VI) (ALTUNA 2004; GERMONPRÉ & SABLIN 2004; BARYSHNIKOV 2006; LIPECKI & WOJTAŁ 2015).

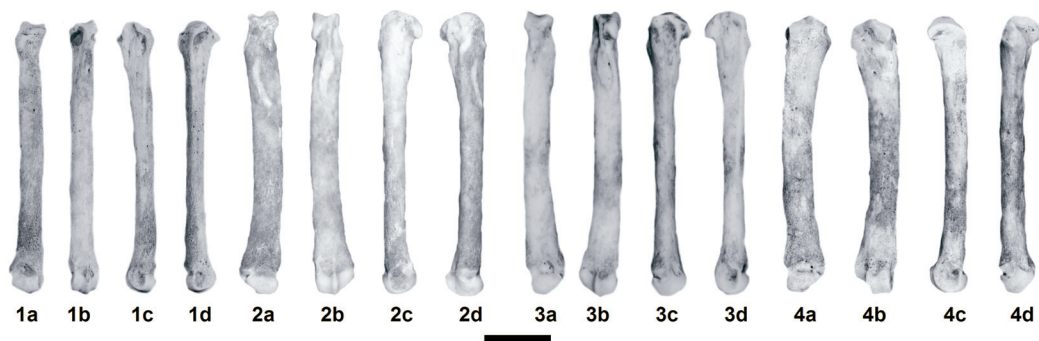


Fig. 12. Red fox *Vulpes vulpes* metacarpals from the Borsuka Cave: left mtc III MF/7073 (1a-d), left mtc II MF/7058 (2a-d), right mtc II MF/7056 (3a-d) and left mtc V MF/7057 (4a-d). All individuals shown to the same scale; a – dorsal view, b – ventral view, c – outer view, d – inner view, scale bar 10 mm.

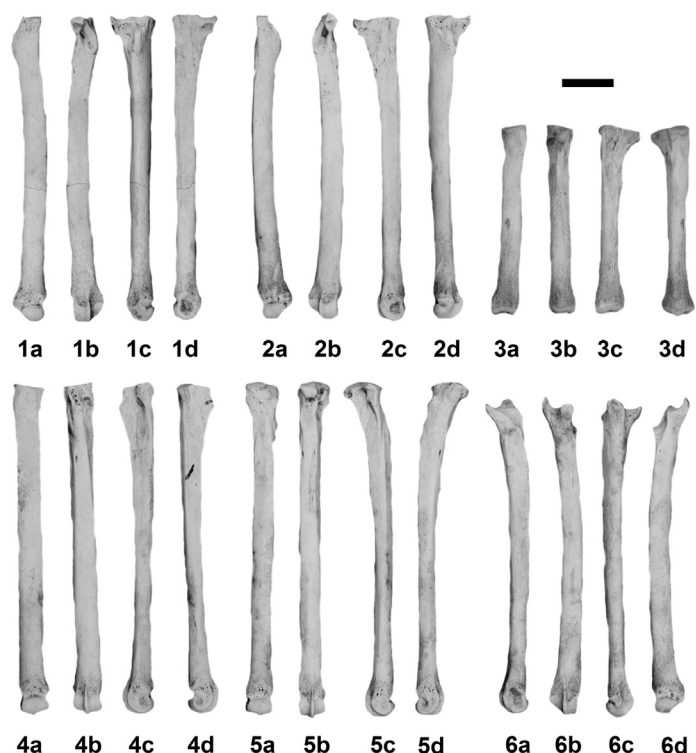


Fig. 13. Metatarsals of *Vulpes vulpes* from the Borsuka Cave: left mtts II MF/7055 (1a-d), right mtts II MF/7059 (2a-d), left mtts III MF/7074 of young individual (3a-d), right mtts III MF/7061 (4a-d), right mtts IV MF/7062 (5a-d) and left mtts V MF/7063 (6a-d), a – dorsal view, b – ventral view, c – outer view, d – inner view. All individuals shown to the same scale; scale bar 10 mm.

The analysis of the measurements of phalanges, which at first glance have a rather small taxonomic value, provided interesting information. The analysis of a large series of phalanges I and II showed that in *V. lagopus* they were more gracile than those of *V. vulpes* (Table VI), even if comparable in total length (Fig. 14) and their proportions are similar to those of the foxes from Kraków Spadzista (LIPECKI & WOJTAL 2015). The scatter plots of the phalanx total length against the smallest diaphyseal breadth show that the fossil sample of both species is rather homogenous. It is also apparent that two phalanges I from the Holocene sediments of Borsuka Cave classified as *V. vulpes* correspond in size to the recent Polish red foxes (Fig. 14).

Ursus arctos LINNAEUS, 1758

The few small fragments of an ursid belonged to large, arctoid bear. The best preserved were two isolated teeth, with morphology typical of the brown bear. On the tricuspid P4 (MF/6977) there are no traces of metaconulus or metaloph (Fig. 15). The buccal margin is almost straight (only delicately concave in its middle part), whereas the lingual, as well as anterior and posterior margins are much rounded. The paracon is large, round and quite low, the metacone is almost equal to it in size, but lower and more oval in shape, the valley

Table VI

Measurements of canid post-cranial bones from the Borsuka Cave (mm). For measurements scheme see Figs 9-10

Species	Coll. no	Bone	1	2	3	4	5	6	7	8
<i>Canis lupus</i>	E6/571	trapezium	11.64	7.45	6.98					
<i>Vulpes vulpes</i>	MF/7009	humerus	124.91	25.22	19.65	9.66	7.92	14.66	20.62	16.17
<i>Vulpes vulpes</i>	MF/7006	radius	114.25	11.70	7.38	9.06	5.22	14.83	9.16	
<i>Vulpes vulpes</i>	MF/7007	radius	114.53	11.32	7.78	8.72	5.36	15.25	8.82	
<i>Vulpes vulpes</i>	MF/7008	ulna	137.02	12.94	6.69	5.88	5.06	5.48	4.53	
<i>Vulpes vulpes</i>	MF/7012	femur	133.82	26.73	10.65	9.06	8.46	21.16	20.86	
<i>Vulpes vulpes</i>	MF/7013	femur		27.12	11.00					
<i>Vulpes vulpes</i>	MF/7010	tibia		24.05	23.22	9.66	9.47			
<i>Vulpes vulpes</i>	MF/7011	tibia			23.54					
<i>Vulpes vulpes</i>	MF/7055	mtcp II	42.89	6.87	4.42	3.26	4.36	5.89	6.27	
<i>Vulpes vulpes</i>	MF/7056	mtcp II	42.76	6.88	4.79	3.62	4.42	5.74	6.36	
<i>Vulpes vulpes</i>	MF/7073	mtcp III	48.79	8.73	5.24	3.38	4.54	5.76	6.19	
<i>Vulpes vulpes</i>	MF/7058	mtts II	59.97	9.22	3.74	4.19	4.63	6.14	6.38	
<i>Vulpes vulpes</i>	MF/7059	mtts II	59.87	9.14	3.42	4.12	4.63	6.16	6.26	
<i>Vulpes vulpes</i>	MF/7060	mtts III		10.28	6.19					
<i>Vulpes vulpes</i>	MF/7061	mtts III	64.80		6.12	3.59	4.86	6.44	6.02	
<i>Vulpes vulpes</i>	MF/7062	mtts IV	65.92	8.76	4.46	3.45	4.36	5.88	5.59	
<i>Vulpes vulpes</i>	MF/7063	mtts V	62.34	6.12	7.78	4.16	4.53	5.82	5.96	
<i>Vulpes vulpes</i>	MF/7107	calcaneus	32.97	13.18						
<i>Vulpes vulpes</i>	MF/7041	pisiform	10.58	5.25	5.72					
<i>Vulpes vulpes</i>	MF/7037	cuboid	14.36	9.82	10.26					
<i>Vulpes vulpes</i>	MF/7038	navicular	9.92	8.11						
<i>Vulpes vulpes</i>	MF/7040	ectocuneiform	10.82	8.09	5.86					
<i>Vulpes vulpes</i>	MF/7043	ph I	23.62	5.22	5.84	3.26	3.11	3.76	4.72	
<i>Vulpes vulpes</i>	MF/7044	ph I	17.72	5.38	6.34	4.78	4.12	4.11	5.18	
<i>Vulpes vulpes</i>	MF/7045	ph II	17.50	4.60	5.14	3.14	3.02	3.62	4.59	
<i>Vulpes vulpes</i>	MF/7046	ph II	12.96	4.58	5.25	2.96	3.62	3.32	4.62	
<i>Vulpes lagopus</i>	MF/6997	scapholunar	12.24	8.04	5.43					

between the two is strongly pronounced. The elongated and oval, low protocon is a well-developed, large cusp, sharply delineated from the remaining part of the crown. Its anterior margin forms a wide, open angle with the posterior margin of the paracon. On the lingual side a delicate crest running from the protocon toward the paracon crosses the valley between the two main cusps. The cingulum is well-developed, but stronger (forming a small crest) in the postero-buccal part of the crown. It represents morphotype A/B, typical of brown bear (Fig. 15).

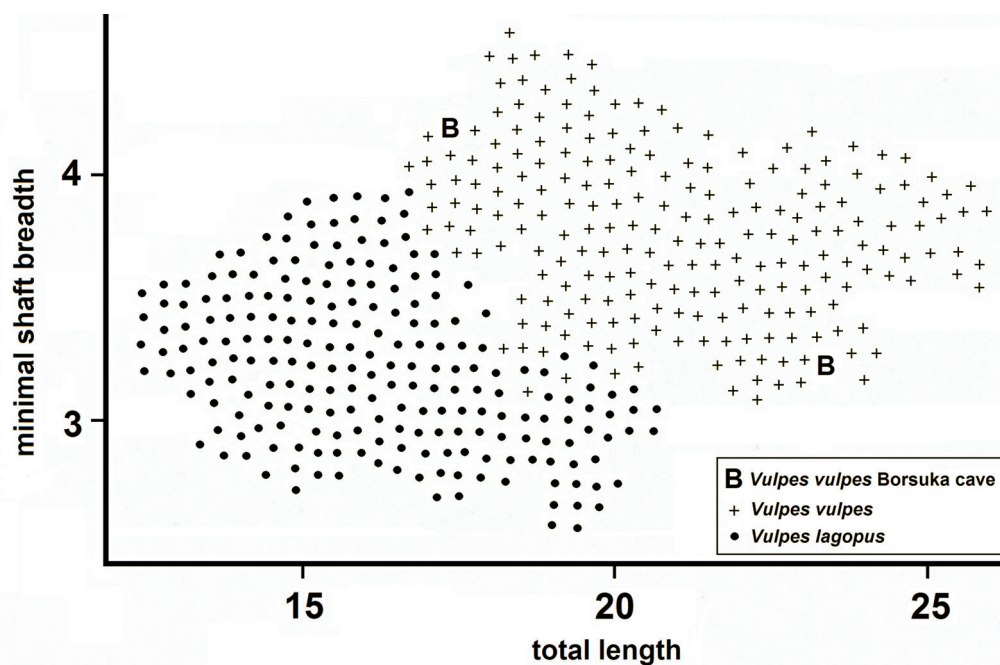


Fig. 14. Total length of phalanx I plotted against minimum shaft breadth of phalanx I in European foxes and in foxes from the Borsuka Cave. Measurements in mm, according to LIPECKI and WOJTAŁ (2015) and own measurements.



Fig. 15. Right P4 MF/6977 of *Ursus arctos arctos* from the Borsuka Cave, a – buccal view, b – lingual view, c – occlusal view, scale bar 10 mm.

The tooth measurements (1 – 18.45 mm, 2 – 10.48 mm, 3 – 14.45 mm) place it above the range of *Ursus arctos arctos*, between large Middle and Late Pleistocene forms: *Ursus arctos taubachensis* and *Ursus arctos priscus* (Fig. 16). However, its simple structure, without any additional cusplets, excluded such taxonomic placement. P4 in those forms is large and broad, proportionally low-crowned and has smaller cusplets: metaconulus, metaloph and/or protoloph. The only reliable explanation is that these remains, dated at the beginning of the Holocene, represented a large brown bear with *priscus*-like features still present in its morphology.

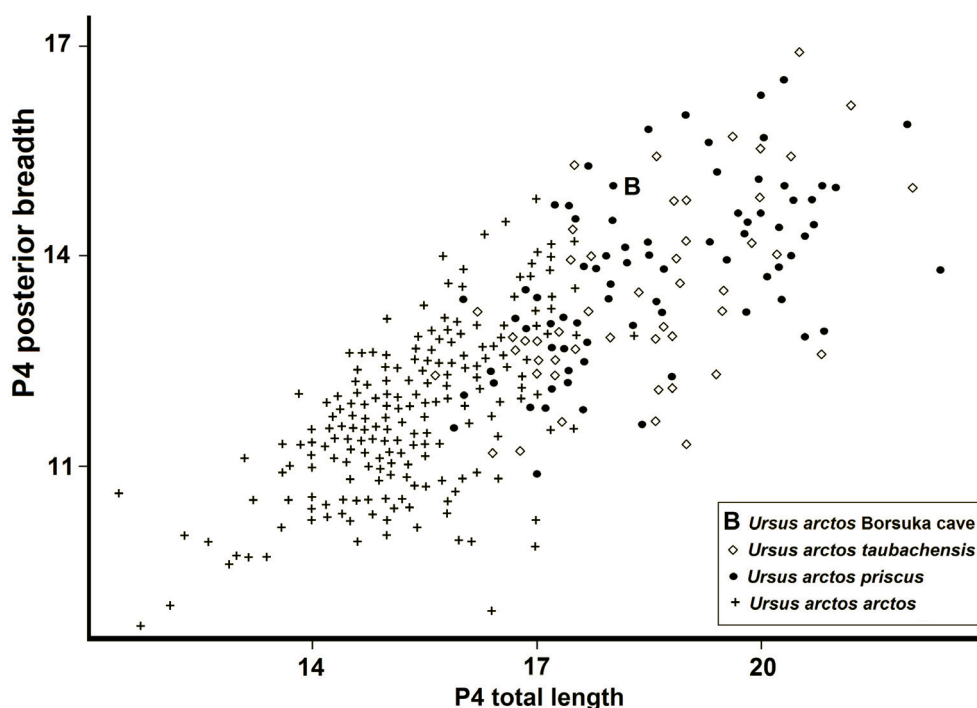


Fig. 16. Total length of P4 plotted against posterior breadth of P4 in different European chronoforms of *Ursus arctos* and in *Ursus arctos arctos* from the Borsuka Cave. Measurements in mm.

The same explanation can be applied to the isolated m3 (MF/6979), found in layer 6 in the Borsuka Cave. Because of the heavy wear, no chewing surface details are distinguishable. Only the outline from occlusal view, representing morphotype C can be discerned. This morphotype rarely occurs in *Ursus arctos arctos*, while it is common in *Ursus arctos priscus* and *Ursus arctos taubachensis*. The measurements of the tooth (1 – 20.52 mm, 2 – 7.16 mm, 3 – 15.22 mm, 4 – 12.94 mm) are within the range of those two forms.

Gulo gulo (LINNAEUS, 1758)

The record of *Gulo gulo* is based on metatarsal II (MF/6976), whose shape and proportions closely resemble other Late Pleistocene remains of the species. Also metrically the bone matches the Late Pleistocene wolverine and exceeds the values for the modern European males (Fig. 17/1a-c, Fig. 18). Large individuals are associated with glacial periods and smaller ones appear during interglacials. The species follows the Bergmann rule (PASITSCHNIAK- ARTS & LARIVIÈRE 1995). The bone also differs from the second metatarsal of *Meles meles* in its much larger size, especially total length and more gracile build, with an elongated shaft and proportionally slim both epiphyses (Table IX). Besides, the proximal end (distal end missing) and the shaft differ morphologically. The shaft proximal to the middle differs from that of the badger in being less cylindrical and roughly triangular in cross-section. This character of shaft usually permits the medullar foramen to be seen in ventral view in *Gulo*, whereas in *Meles* the foramen is usually hidden in this aspect and can

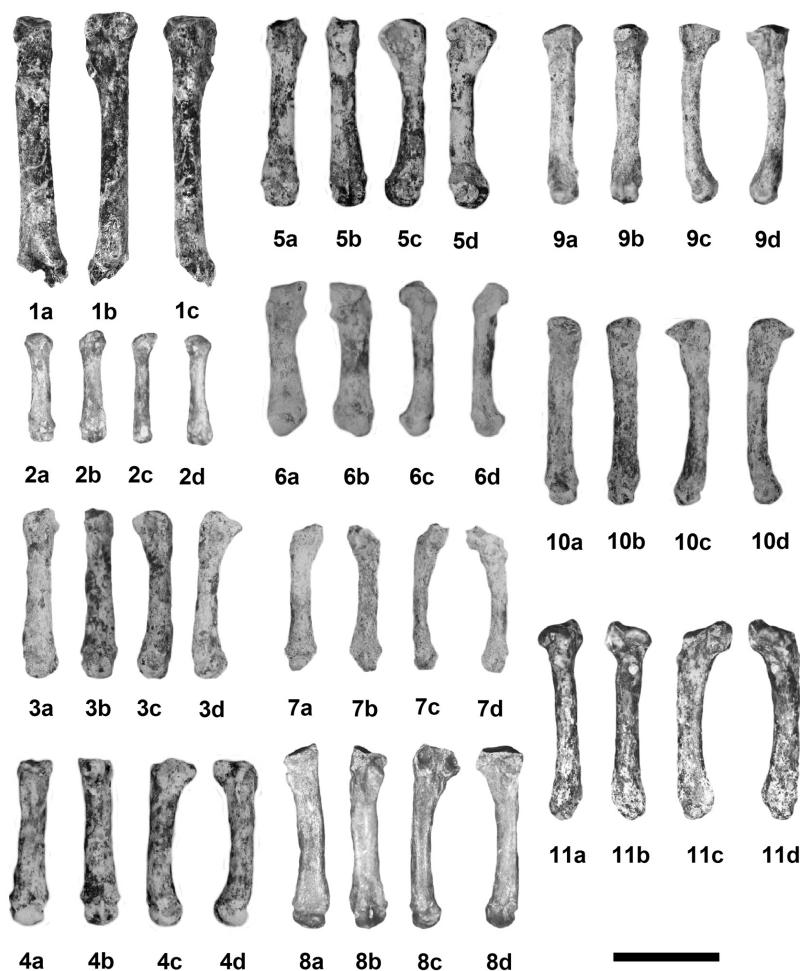


Fig. 17. Metacarpals of large mustelids from the Borsuka Cave. *Gulo gulo*: right mts II MF/6976 (1a-d) and *Meles meles*: left mtcp I MF/6916 (2a-d), left mtcp II MF/6934 (3a-d), left mtcp III MF/6913 (4a-d), left mtcp V MF/6909 (5a-d), left mts I MF/6923 (7a-d), left mts II MF/6915 (8a-d), left mts III MF/6933 (9a-d), right mts IV MF/6907 (10a-d) and left mts V MF/6908 (11a-d), a – dorsal view, b – ventral view, c – outer view, d – inner view. All individuals shown to the same scale; scale bar 20 mm.

be seen best when the metapodial is viewed from the inner side. The rugose tendinal area on the ventral side below the proximal end appears to be more conspicuous in *Meles* and often extends farther down the shaft than in *Gulo*. When viewed from the side, the shaft is seen to be slightly more curved in *Meles* than in *Gulo*. The ventral arm of the hammer-shaped facet for the entocuneiform is shorter. In *Gulo* the proximal end of the bone exhibits a greater extent of bone lying ventral to this facet than in *Meles*. Frequently in *Gulo* the dorsal facet for articulation with mts III reaches back to the proximal end of the bone, and the ventral facet, also for mts III, does not reach the proximal end. In *Meles* the situation is reversed for these two surfaces. The border of the median ventral keel of the distal articulation, when viewed from the side, is quite straight in *Gulo*, as in the specimen from the Borsuka Cave. In *Meles* the keel usually curves dorsally and the border is convex (Fig. 17/1a-c).

Meles meles (LINNAEUS, 1758)

The most abundant species – badger – is represented among other remains by a slightly damaged skull MF/6950 which belonged to a young adult animal. The measurements (all in mm) confirmed it clearly: **1** – 124.61, **2** – 121.81, **3** – 112.89, **4** – 64.85, **5** – 57.09, **6** – 71.89, **7** – 39.07, **8** – 51.89, **9** – 68.06, **10** – 20.20, **11** – 34.22, **13** – 19.30, **14** – 30.40, **15** – 40.87, **16** – 43.22, **17** – 20.86, **18** – 31.28, **19** – 27.94, **20** – 32.37, **21** – 25.97, **22** – 51.28, **23** – 63.94, **24** – 30.65, **25** – 20.04, **26** – 17.27, **27** – 13.34, **28** – 17.67, **29** – 23.97, **30** – 20.84, **31** – 43.79, **32** – 39.87, **33** – 51.32. The animal had permanent dentition, of which only P4 (**1** – 8.94, **2** – 7.82, **3** – 4.86) and M1 (**1** – 14.76, **2** – 12.27, **3** – 10.62, **4** – 10.11) were present. The morphology and measurements of the specimen indicate a young female in the first age class. The long and well-developed, but low sagittal crest and the incompletely fused sutures and epiphysis confirmed the young age of the individual. The tooth (only P4 is present) is almost intact, without any signs of wear, which suggests an animal younger than one year. In the badger sexual dimorphism is pronounced: males are larger and heavier than females. Also skulls and post-cranial bones in adult males are longer and more robust. The examined specimen is quite small. Its total skull length, ca. 125 mm, falls in the lower range of the modern European badgers. Usually, female skulls do not exceed 135–140 mm in total length (MARCISZAK 2012).

The size and morphology of the preserved dentition of *Meles* from Borsuka cave are typical of the species (able VII), and the young age of most teeth makes it possible to examine their structure. The I3 is single-rooted and labio-lingually elongated, with most of the crown consisting of a large cusp that is deflected lingually and compressed labio-lingually, resulting in a blade-like form. The blade arches slightly labially in occlusal view. The mesial edge of the main cusp is about half as long as the distal one. The cingulum, quite well-developed mesio-lingually and distally, is continuous with the mesial edge of the main cusp. The distal cingulum is less developed and not so long, bulging out into a minor cusplet at the place of contact with the posterior edge of the main cusp.

The triangular P4 has a slightly convex buccal margin and is slightly concave lingually. The paracon is the largest and the highest cusp, which is compressed bucco-lingually and has three thin, but well-defined ridges running from its top to the base of the cusp. The antero-lingual ridge is rounded and blunt, while the antero-buccal and posterior ones, which constitute the anterior part of the P4 blade, are more trenchant. The low metacon is slightly curved buccalo-posteriorly, while the metastyl is somewhat swollen. The buccal margin is little depressed in its median part, and ended with a well-developed, quite thick cingulum.

The trapezoid M1 has a low crown with mostly convex margins. The two main cusps, the paracon and the metacon, are equal in size, but the paracon is higher. The top of the paracon is situated anteriorly to the midpoint of its antero-posterior length, while in the metacon the peak culminates more posteriorly to the midpoint of its length. Both the main cusps are compressed buccalo-lingually, resulting in a blade-like form, and divided by a well defined, V-shaped deep valley. The paracon blade in its anterior direction passes into a minute parastyle ridge, while the metacone base posteriorly passes into a metastyl. A fine, sharply distinguishable cingulum surrounds the antero-buccal margin of the crown.

The crest on the lingual side is elongated and well-developed, starting from the anterior base of the paracon and the parastyl connection, and posteriorly exceeds considerably the

Table VII

Mandible and teeth dimensions of mustelids from the Borsuka Cave (mm). For measurements scheme see Fig. 5 (for mandible) and Fig. 6 (for teeth)

Measurements		<i>Meles meles</i>	<i>Mustela nivalis</i>	
		MF/6942	MF/6973	MF/6974
Mandible	3		8.12	
	4		6.58	
	5		6.94	
	6		3.58	
	7		3.78	4.19
	8	3.25	1.22	1.29
	12	15.52	2.08	2.76
	13	8.32	1.06	1.42
	14	17.78	2.00	2.86
	15	8.64	1.07	1.22
p4	L		1.65	1.87
	Ba			0.94
	Bp			0.99
m1	L		3.16	3.76
	L tri		2.18	2.68
	L tal		0.98	1.08
	B tri		1.02	1.32
	B tal		0.98	1.27
m2	L		0.54	
	B		0.55	

length of the metastyl. The crest is formed by a row of four elevations whose size increases in the anterior-posterior direction. All four elevations are separated from one another by deep, narrow valleys. Near the smallest, anteriormost elevation on the antero-buccal side there is situated a small, but well-defined paraconul. From its base a short and sharp ridge runs in the posterior direction and disappears into the lingual base of the paracon. The protocon is formed by the largest, posteriormost elevation.

The large metaconul, of the same size as the protocon, is positioned postero-buccally to the protocon and postero-lingually to the metacon, and it is clearly separated from both these cusps by deep valleys. The V-shaped valley situated between the metaconul and the metacon runs into the trigon basin, while the U-shaped valley separating the metaconul and the protocon is much more spacious. As a result a very low threshold distinguishes the

trigon surface from the talon posterior basin. Four thin and sharp ridges run from the centrally positioned top of the metaconul; they reach the one cusp base so that the whole cusp resembles an isosceles triangle. The most expanded and posterior wall is convex, forming a concave posterior margin in front of and behind the metaconul in occlusal view. Two posterior ridges, demarcating the posterior wall are sharper than the blunter anterior ones. The antero-buccal ridge reaches the metacon lingual base at the midpoint of the valley length separating the metaconul and the metacon. The postero-buccal ridge forms a saddle between the metaconul and the metacon, which posteriorly closes the valley separating these two cusps. In the distal direction, after passing this saddle, the ridge vanishes into the posterior base of the metacon and the buccal side of the metaconul. Between these two long ridges, located on the basal surface of the metaconul anterior wall there is a sharp, thin and short ridge, which runs to the bottom of the valley between the metaconul and the metacon. This ridge vanishes into the metacon base. The antero-lingual metaconul ridge links it with the protocon along the threshold separating the trigon and talon surfaces.

The talon is much broader and more expanded anteriorly and posteriorly than the trigon. In occlusal view it is noticeably convex in the mesial direction. The lingual margin is strongly concave at about the midpoint of its antero-posterior length, which separates the talon surface in two parts: anterior and posterior. This lingual outline is surrounded by a very thick and high, almost continuous cingulum which starts in the paraconul anterior base and ends in a V-shaped notch, where it connects with the posterior-lingual ridge of the metaconul. This thick cingulum ridge on occlusal side forms a few small and two larger elevations located one behind the other. The lingualmost are the smallest, while the buccalmost are the largest. Among the small elevations, four cone-like ones flank the anterior surface, while the other three flank the posterior surface. A distinct, V-shaped notch borders the buccal and the medial elevations of the posterior row. The other elevations are also more or less isolated by shallower, V-shaped valleys. The grooves separating the small elevations located the lingualmost from the large cingular elevations are thin but well-visible. These large elevations constitute notably large and thick ridges that surround the lingual margin of the anterior and posterior surfaces of the talon. They are separated by a broad depression at the level of the concavity in the talon lingual margin. The posteriorly located hypocon is oriented antero-lingually and connects with the posterior large elevation, which ends in a sharp bulge, forming a tapered tip. There is a discontinuous, thin cingulum running along the lingual margin from the level of the top of posterior large elevation and ending in the notch between the lingual and medial posterior small elevations. The talon surface is divided into three depressions, where the anterior and the medial one are separated from each other by a low threshold which connects the anterior large elevation of the cingulum with the medial large elevation of the trigon lingual crest. Another low threshold separates the medial and the posterior depressions, and connects the protocon posterior part with the posterior large cingular elevation. The numerous post-cranial bones of *Meles meles* are easily distinguished from other mustelid remains based on their relatively large size and massive build, while they differ from the bones of *Gulo gulo* in their smaller dimensions and stout build (Tables VIII-IX). Especially the well-preserved and numerous metacarpals and metatarsals are proportionally short and massive, with robust both epiphysis (Fig. 17/2a-d to 11a-d). Their measurements fall far below the minimum total length of the wolverine metapodials (Fig. 18).

Table VIII

Measurements of isolated mustelid teeth from the Borsuka Cave (mm). Measurements of teeth according to VON DEN DRIESCH (1976)

Species	Coll. no	Tooth	L	B
<i>Meles meles</i>	MF/6917	C1	8.04	5.94
<i>Meles meles</i>	MF/6924	i3	5.00	5.22
<i>Meles meles</i>	MF/6905	c1	9.20	5.95
<i>Martes martes</i>	MF/6968	p4	5.97	3.06
<i>Martes martes</i>	MF/6969	c1	7.14	4.67
<i>Mustela erminea</i>	MF/6989	m1	5.37	[1.90]
<i>Mustela nivalis</i>	MF/6972	P4	3.34	1.39

Table IX

Measurements of mustelid post-cranial bones from the Borsuka Cave (mm). For measurements scheme see Figs 9-10

Species	Coll. no	Bone	1	2	3	4	5	6	7	8
<i>Gulo gulo</i>	MF/6976	mtts II	[52.00]	6.93	9.97		7.03			
<i>Meles meles</i>	MF/6910	humerus				14.48	11.39	23.49	40.58	33.10
<i>Meles meles</i>	MF/6911	humerus	102.74	27.28	23.57	10.27	9.27	15.52	28.62	20.16
<i>Meles meles</i>	MF/6932	humerus				12.04	10.36	15.78	30.08	22.54
<i>Meles meles</i>	MF/6951	radius		12.24	8.18	6.90	5.29			
<i>Meles meles</i>	MF/6926	radius				6.45	5.25	17.26	12.22	
<i>Meles meles</i>	MF/6920	radius	91.97	13.65	9.89	4.36	6.16	13.43	9.93	
<i>Meles meles</i>	MF/6929	femur		27.64	11.82	9.92	10.58			
<i>Meles meles</i>	MF/6927	tibia				6.98	9.86	19.07	12.14	
<i>Meles meles</i>	MF/6916	mtcp I	20.52	4.78	4.99	2.79	3.51	3.86	4.87	
<i>Meles meles</i>	MF/6934	mtcp II	30.54	8.12	5.48	3.62	4.32	6.64	6.32	
<i>Meles meles</i>	MF/6921	mtcp II	26.74	7.63	5.29	3.86	4.44	6.04	6.27	
<i>Meles meles</i>	MF/6913	mtcp III	29.02	7.09	4.98	3.98	4.52	6.19	6.19	
<i>Meles meles</i>	MF/6922	mtcp III	35.04	9.89	7.63	5.26	5.87	8.87	8.78	
<i>Meles meles</i>	MF/6954	mtcp III	26.53	7.14	5.63	3.36	4.12		5.98	
<i>Meles meles</i>	MF/6909	mtcp V	27.84	8.73	7.84	3.45	4.98	6.22	7.32	
<i>Meles meles</i>	MF/6923	mtts I	26.63	6.62	6.89	3.81	4.87	5.52	5.96	
<i>Meles meles</i>	MF/6915	mtts II	32.87	8.49	6.42	3.96	4.96	5.97	7.41	
<i>Meles meles</i>	MF/6912	mtts III	32.94	7.74	7.14	3.66	4.42	5.84	6.17	
<i>Meles meles</i>	MF/6933	mtts III	30.60	7.89	6.24	3.34	4.47		6.57	
<i>Meles meles</i>	MF/6907	mtts IV	33.00	8.12	7.29	3.66	4.52	5.45	6.02	
<i>Meles meles</i>	MF/6908	mtts V	30.10	6.78	6.94	3.22	4.38	5.65	6.84	
<i>Meles meles</i>	MF/6925	mtts V	33.69	7.69	7.97	3.54	4.36		6.69	
<i>Meles meles</i>	MF/6914	calcaneus	29.97	15.14						
<i>Meles meles</i>	MF/6958	ph II	10.17	4.78	6.16	2.52	4.42	4.22	4.66	
<i>Mustela sp.</i>	MF/6971	femur	56.45	13.29	5.82	4.49	4.12	9.84	12.97	

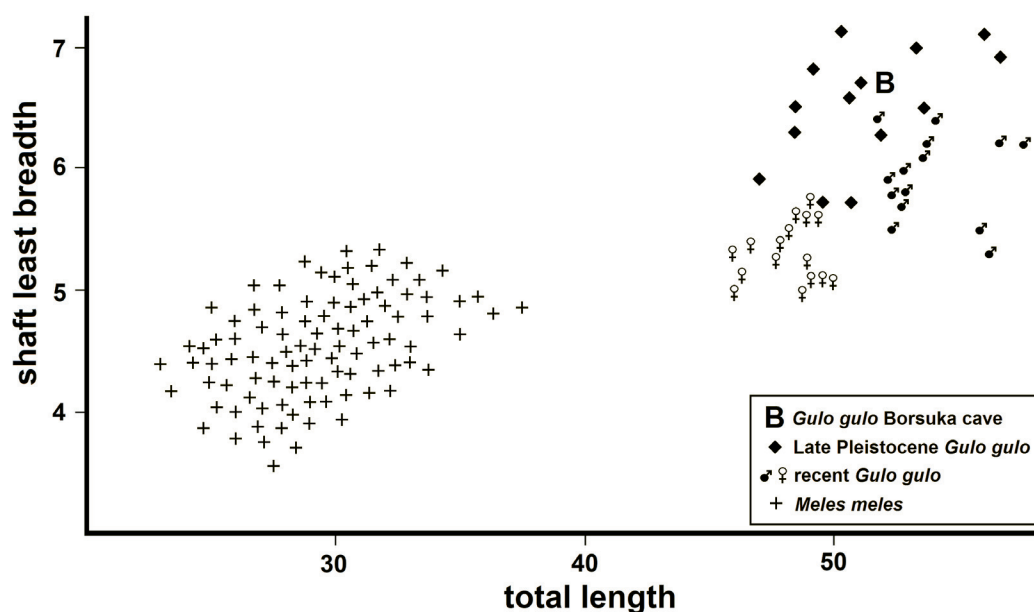


Fig. 18. Total length of metatarsal II plotted against minimum shaft breadth of metatarsal II in European large mustelids *Gulo gulo* and *Meles meles*, and in *Gulo gulo* from the Borsuka Cave (marked as B on the graph). Measurements in mm, according to DÖPPES (2001); LIPECKI & WOJTAL (2015) and own data.

Martes martes (LINNAEUS, 1758)

Three isolated teeth, a single canine and two p4, represented *Martes martes*. Metrically and morphologically those remains are indistinguishable from corresponding teeth of the pine marten (Table VIII). Since *Martes martes* is a classical example of Bergmann's rule, whereby larger individuals are found in colder climates, and those of smaller size are found in warmer regions or during warmer periods, the single canine from the Borsuka Cave belonged to a large-sized specimen. MARCISZAK (2012) reported the following values of c1 length in individuals from recent Polish populations: mean for males 5.83 mm (4.81–6.65 mm, n=163), and mean for females 4.24 mm (3.74–5.14 mm, n=108). With its crown length of 7.14 mm the tooth MF/6969 considerably exceeds the dimensions of the modern Polish pine marten and corresponds to the robust Late Pleistocene individuals (5.97 mm, 5.70–7.78 mm, n=22). Contrary to c1, the single p4 MF/6968 is quite small and narrow, and indicates a medium-sized marten. Based on an abundant sample from the modern Polish population, MARCISZAK (2012) reported the following values for p4: mean for males 6.14 mm (5.12–6.78 mm, n=157), and a mean for females 5.48 mm (4.87–6.06 mm, n=108). The teeth described above differ from those of *Martes foina* in the relatively longer and less curved crowns of c1 and the narrower crown with a less pronounced additional cusplet located postero-buccally to the protoconid.

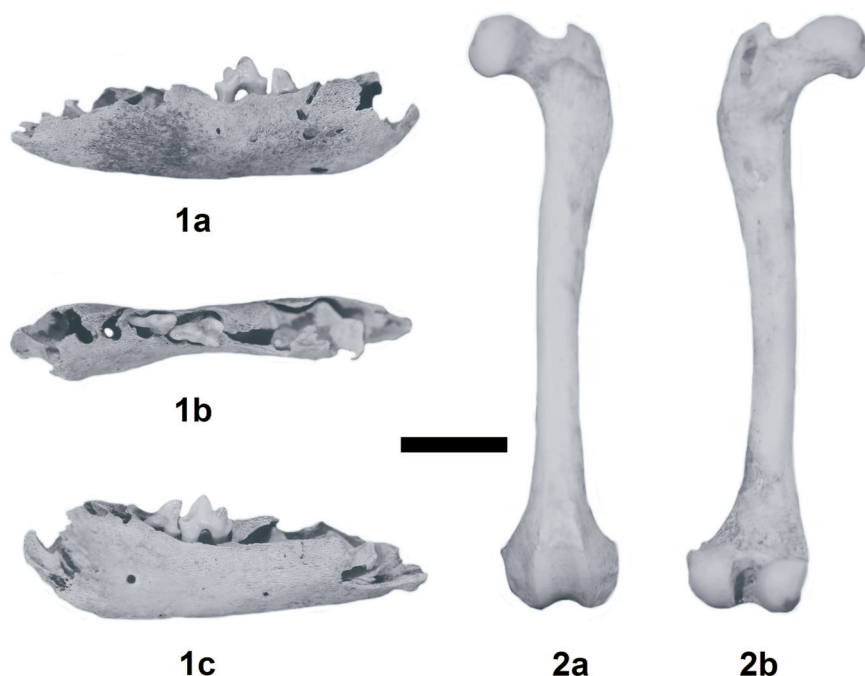


Fig. 19. Remains of an undetermined polecat *Mustela* ex. gr. *eversmanii-putorius* from the Borsuka Cave: right mandible of young animal MF/6970 (1a – buccal view, 1b – occlusal view, 1c – lingual view) and left femur MF/6971 (2a – dorsal view, 2b – ventral view. Both individuals shown to the same scale; scale bar 10 mm.

Mustela ex. gr. *eversmanii-putorius*

Besides *Martes martes*, medium-sized mustelids from the Borsuka cave are also represented by an undetermined polecat classified as *Mustela* sp. (ex. gr. *eversmanii-putorius*) (Fig. 19). Two polecat species occur in Poland in the Pleistocene deposits and today: *Mustela eversmanii* and *M. putorius*. Although similar in metric and morphological values, they differ in many features, which have been intensively studied by many authors e.g. NEHRING (1904); KOKEN (1912); WURM (1913); KORMOS (1916); SOERGEL (1917); ŽELÍZKO (1917); EHIK (1928); MOTTI (1937); KRETZOI (1942); KOBY (1951); MALEZ (1963); HEPTNER (1964); HEPTNER & NAUMOV (1967); REMPE (1970); GAUTIER (1980); POHAR (1981); DELPECH (1989); SPASSOV & SPIRIDONOV (1993); WOLSAN (1993a, 1993b); FOSSE & FOURVEL (2010), MARCISZAK (2012) and KRAJCARZ et al. (2015a). Most distinctive features are provided by the calvarium and mandible, as well as teeth; especially carnassials and molars differ clearly. Direct measurements are not very useful in polecat identification. *M. eversmanii* is on average larger, the mean values differ between the two species, but the extreme values are almost the same. Because of the pronounced sexual dimorphism, with adult males twice or more heavier and much larger than females, size differences provide no reliable information besides sex determination. All found differences are taxonomically valuable, when the analysed material is represented by adult specimens. However, the very young age and deciduous dentition of the mandible from the Borsuka Cave make the identification impossible (Fig. 19/1a-c).

In the Borsuka Cave also a complete femur of the polecat was found (Fig. 19/2a-b), and findings of long bones of the genera *Martes* and *Mustela* are quite common in archeological and paleontological sites. Despite the fact that the bone is adult and complete, as in the case of the above-described mandible it is almost impossible to identify it precisely. The metric and morphological similarity between polecats is so great that post-cranial material is usually referred to as *Mustela* sp. Although some authors (GALIK 1996, 1997) tested metric differences in proportions and morphology of long bones, their attempts were based on a relatively scanty material, not reflecting the large size variation in the two species. Morphological differences pertain mainly to the humerus (KOBY 1951; GALIK 1997; MALLYE and GUÉRIN 2002). The femur from Borsuka Cave is particularly large and robust and belonged probably to an adult male (Fig. 19/2a-b).

***Mustela erminea* LINNAEUS, 1758 and *Mustela nivalis* LINNAEUS, 1766**

The two smallest mustelids from Borsuka Cave, *Mustela erminea* and *Mustela nivalis*, are represented by relatively small material, the best preserved remains being two mandibles of the least weasel (Fig. 20). Distinguishing small members of the genus *Mustela* in the fossil material is difficult, especially when the material is small and/or incomplete. The most valuable criterion is the larger size of *M. erminea*, though it is not always reliable because of the pronounced sexual dimorphism (males of smaller species are sometimes larger than females of larger species), the geographical variation, and the effect of altitude and local environmental conditions. Late Pleistocene members of *Mustela*, especially those from cold periods, were on average smaller than the individuals from warmer periods (WÓJCIK 1974; MARCISZAK 2012). One isolated m1 from the Borsuka Cave, with the total crown lengths of m1 of 5.37 mm (MF/6989) (Table VIII), represented *M. erminea*, while the two much smaller mandibles from the same site, with m1 3.16 mm (MF/6973) and 3.76 mm (MF/6974) long, were determined as *M. nivalis*. The larger values in both species most probably represented males, the smaller ones – females. Additionally the relatively small

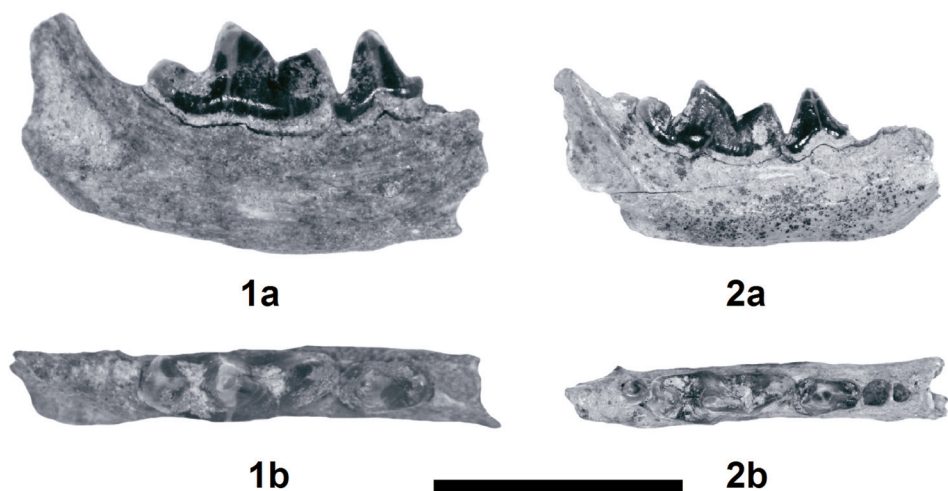


Fig. 20. Remains of least weasel *Mustela nivalis* from Borsuka Cave: right mandibles MF/6974 (1a-b) and MF/6973 (2a-b), a – buccal view, b – occlusal view. Both specimens shown to the same scale; scale bar 5 mm.

size and gracile build suggest that their morphology reflected adaptation to colder environmental conditions. These small individuals of both species are metrically and morphologically indistinguishable from modern dwarf individuals which occur in Arctic regions.

Also other metric values proved to be reliable diagnostic criteria to distinguish between the stoat and the least weasel. *M. erminea* is characterised by a proportionally broader posterior part of the p4 crown, a longer trigonid, a strongly pronounced broadening of the m1 crown situated at the protoconid level, and a narrower and shorter talonid (Fig. 21). The mean length ratio of talonid to trigonid for *M. erminea* is 23.4, for *M. nivalis* it is 41.2. This ratio for the specimens from the Borsuka Cave is 28.3 (MF/6989) for *M. erminea* and 45.0 (MF/6973) and 40.3 (MF/6974) for *M. nivalis*. At the same time, the mean breadth ratio of talonid to trigonid is 76.0 for *M. erminea* and 92.1 for *M. nivalis*. The values obtained for the specimens from the Borsuka Cave clearly separated the stoat remains from the least weasel remains, with 96.1 (MF/6973) and 96.2 (MF/6974) for *M. nivalis*.

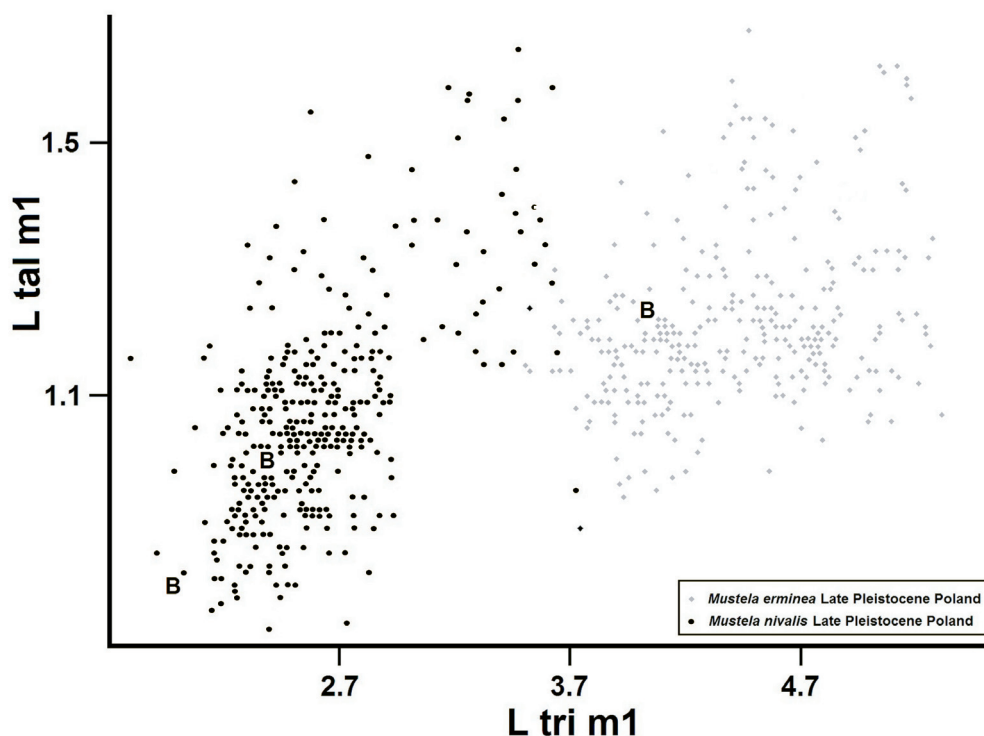


Fig. 21. Talonid length of m1 (L tal m1) plotted against trigonid length of m1 (L tri m1) in *Mustela erminea* and *Mustela nivalis* from the Late Pleistocene of Poland (B – data from the Borsuka Cave). Data from MARCISZAK (2012) and references therein, measurements in mm.

Lynx lynx (LINNAEUS, 1758) and *Felis silvestris* SCHREBER, 1777

The faunal assemblage is completed by two felid species. *Lynx lynx* is represented by a damaged right phalanx I-1-a (MF/6975), which is metrically (1 – 17.22 mm, 2 – 8.15 mm, 3 – 10.74 mm, 4 – 7.82 mm, 5 – 7.57 mm) and morphologically indistinguishable from the corresponding phalanx of the modern European lynx. The smaller felid, *Felis silvestris* is represented,

among other remains, by a left mandible body (MF/6964). The animal had permanent dentition and was fully grown; the measurements indicate a medium-sized individual (5 – 29.94, 7 – 6.49, 8 – 23.76, 9 – 15.22, 16 – 10.79, 17 – 5.59). All the cheek teeth are present: p3 (1 – 7.00, 2 – 4.44, 3 – 4.84, 4 – 2.39, 5 – 3.14), p4 (1 – 8.48, 2 – 4.28, 3 – 5.86, 4 – 3.17, 5 – 3.74) and m1 (1 – 8.86, 2 – 4.47, 3 – 5.08, 4 – 5.01, 5 – 5.69, 6 – 3.36, 7 – 3.98). In all likelihood the two isolated lower canines (MF/6965 with dimensions of 5.78 x 4.32 mm and MF/6962 with measurements of 5.87 x 4.19 mm) belonged to the same animal. The complete metatarsal III MF/6966, assigned to the same animal, with the measurements (all in mm): 1 – 55.33, 2 – 9.00, 3 – 7.21, 4 – 3.64, 5 – 5.14, 6 – 6.36, 7 – 6.49, also indicates a medium-sized individual.

Because of the uniform morphology and great variation of small felids, it is always difficult to distinguish between the species and forms. Besides, the findings dated as MIS 1 are additionally complicated by the occurrence in the fossil material of the feral cat, a form created by man (KRAJCARZ et al. 2015b). In the past many authors tried to find statistically reliable features which would allow separating the wildcat and the feral cat (SUMIŃSKI 1962; KRATOCHVÍL 1973, 1976; HEMMER 1993; KITCHENER et al. 2005). However, detailed metric and morphological analyses of large samples of both forms from archaeological and palaeontological sites showed that virtually no measurements or ratios can be regarded as reliable. Even when mean values differ, the ranges still overlap. On average *Felis silvestris* is larger and more robust, however the feature is not completely diagnostic. The great intraspecific variation, sexual dimorphism and above all hybridisation between the two forms, especially frequent during the last 2 ka render their identification very difficult. In this context morphological features proposed by KRATOCHVÍL (1973, 1976) are more valuable than measurements. The specimen from Borsuka Cave is not very large and rather robust (Fig. 22). The massive mandible with large m1 (length exceeding 8.0–8.5 mm

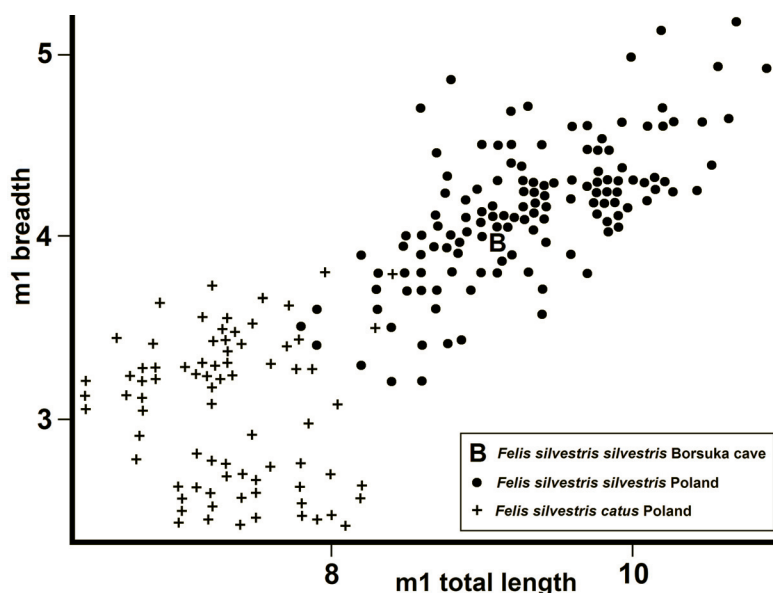


Fig. 22. Total length of m1 plotted against m1 breadth in the wildcat *Felis silvestris silvestris* and the feral cat *Felis silvestris catus* from the postglacial and Holocene of Poland and the wildcat from the Borsuka Cave (indicated at the graph by B). Own data, all measurements in mm.

in subfossil finds almost exclusively representing wildcat) is more typical of the wildcat, and the specimen was identified accordingly.

IV. DISCUSSION

The carnivore remains from the Borsuka Cave represent 12 species: *Canis lupus*, *Vulpes vulpes*, *Vulpes lagopus*, *Ursus arctos arctos*, *Gulo gulo*, *Meles meles*, *Martes martes*, *Mustela ex. gr. eversmannii-putorius*, *Mustela erminea*, *Mustela nivalis*, *Lynx lynx* and *Felis silvestris*. They are common components of the Late Pleistocene and Holocene faunal assemblages of Central Europe (KOWALSKI 1959; WOLSAN 1989; WOJTAL 2007; NADACHOWSKI et al. 2015; STEFANIAK 2015; LIPECKI & WOJTAL 2015; WILCZYŃSKI et al. 2016; MARCISZAK et al. 2017). The carnivore remains from the Borsuka Cave represent two different faunal assemblages. The younger one comes from the Holocene layers I-IV, while the older one was found in layers VI-VII of Late Pleistocene age. The material from the younger layers is poorer in species but richer in terms of the number of remains and specimens. Deposition during that period could be associated with both animal and human activities during the last 8 ka.

The older assemblage (layers VI-VII) provided a rich and diverse fauna. Its composition, the traces of carnivore activity (gnawing marks and digested bones) and the lack of traces of human activity (cut marks, burnt bones) indicate natural character of this bone accumulation. Layers I-II contained numerous remains of *Vulpes vulpes* (adult and young individuals), together with few bones of a wildcat and a badger. The remains of *Meles meles* and *Felis silvestris* indicate the presence of deciduous forests in the environs of the cave during the deposition (WILCZYŃSKI et al. 2012a). The layer III was dominated by *Meles meles*; the accumulation of its remains appears to have been natural. The layer V corresponds with the significant cooling of the climate associated with the Last Glacial Maximum and is almost devoid of archaeological or paleontological material. The most interesting faunal assemblage was found in layer VI, whose accumulation was associated with carnivore activity. Though the fauna included cold-loving species such as *Vulpes lagopus*, *Gulo gulo* and *Mustela erminea*, and those associated with a warmer, forest environment: *Meles meles* and *Martes martes*, it was dominated by euryoecious forms which could live in both kinds of habitats.

The euryoecious Late Pleistocene wolf is sometimes regarded as a distinct ecomorph *C. lupus spelaeus* (GOLDFUSS 1823). This form is mentioned from different European sites, but usually only briefly and almost never described in detail (DIEDRICH 2014). The form/subspecies category tends to be employed rather freely in the canid palaeontology. A preliminary analysis, however, indicates that the form differed somewhat in its morphology from the Holocene and modern specimens of *Canis lupus*. Apart from the larger average size, it was also characterised by broader teeth and more robust post-cranial bones (BOUDADI-MALIGNE 2012; SANSALONE et al. 2015). These differences require a more detailed analysis (MARCISZAK et al. 2017).

Another euryoecious species, the brown bear, is adapted to a range of climate conditions and habitats, including cold steppe-tundra (MUSIL 1964, 1996; SABOL 2001a, 2001b; PACHER 2007; MARCISZAK et al. 2015; LIPECKI & WOJTAL 2015). It was recorded from

various cave and open-air sites of both the Late Pleistocene and the Holocene of Poland (MARCISZAK et al. 2015; NADACHOWSKI et al. 2015; WOJTAL et al. 2015; MARCISZAK et al. 2017). The ursid remains from the Borsuka Cave belong to the robust brown bear, whose large size reflects its association with the cold periods, even if the date suggested already a Holocene age.

The occurrence of two species, *Vulpes lagopus* and *Gulo gulo*, in the layer VI indicates cool conditions and a steppe-tundra and/or tundra-open boreal forest biome near the site during the deposition. The polar fox is a circumpolar species, well adapted to cold conditions. Usually a tundra-dweller, it may also penetrate the boreal forest zone during its winter migrations (SHELDON 1992; KAHLKE 1999; BARYSHNIKOV 2006). During the Late Pleistocene the species was widespread in Europe (KAHLKE 1999), the maximum extent of its distribution range reaching the northern part of the Iberian Peninsula in the southwest (ÁLVAREZ-LAO & GARCIA 2011). Today *Vulpes lagopus* in Europe is restricted to the tundra regions of Fennoscandia (BARYSHNIKOV 2006). Due to climate warming the red fox wanders much more to the north than previously and aggressive encounters with the polar fox are not uncommon. Usually when they meet, the larger *Vulpes vulpes* dominates and sometimes even kills a smaller *Vulpes lagopus* (PAMPERIN et al. 2006). The same scenario is also not excluded for the vicinity of the Borsuka Cave at the time, when the more thermophilic red fox re-colonised after cold period, and when the polar fox was still present (Fig. 23). Its fossil records from Poland are numerous and dated mostly as the Late Pleistocene (WOLSAN 1989; CYREK et al. 2000; WOJTAL 2007; MARCISZAK et al. 2011; NADACHOWSKI et al. 2015; LIPECKI & WOJTAL 2015; WILCZYŃSKI et al. 2016).



Fig. 23. Aggressive encounter between the red fox *Vulpes vulpes* (on the left) and the polar fox *Vulpes lagopus* (on the right) in the vicinity of the Borsuka Cave. In general in canids, the larger species tends to dominate on the smaller one. Drawing by W. GORNIG.

The wolverine is only defined as a northern element of boreal (taiga-type) forests. In modern times however it also lives in open tundra lowlands as well as at high mountain altitudes, which suggests that it inhabited also the open steppe-tundra (PASITSCHNIAK-ARTS & LARIVIÈRE 1995). Recently the wolverine in Europe is restricted to the areas extending from eastern Europe to the northern parts of the Scandinavian Peninsula, while in the Late Pleistocene its range was much more extensive, reaching as far as the northern part of the Iberian Peninsula in the southwest (DÖPPES 2001).

The oldest remains of *G. gulo* come from the lowermost layers of the Biśnik Cave (layer 19ad) (MARCISZAK et al. 2011). Based on biochronological data, those lowermost layers are estimated as MIS 10-9 (KRAJCARZ et al. 2014; MARCISZAK 2014). A few isolated teeth from layers 1 and 3 of the Deszczowa Cave are somewhat younger (MIS 6) (KRAJCARZ 2012; KRAJCARZ & MADEYSKA 2012). *Gulo gulo* from all three above-mentioned, late Middle Pleistocene sites are morphologically distinct from those of Late Pleistocene age. They represent a more primitive form, of a smaller size and slighter build.

The most numerous records come from the Late Pleistocene, when the species was widespread in Europe. Most of them are reliably dated the last glacial (MIS 5d-MIS 2). The remains were found in the Deszczowa Cave (left mandible with p2-m2 and some post-cranial bones of a female, layers 8 and 9, MIS 2) (WOJTAL 2007); the Nietoperzowa Cave (fragment of left mandible with p3-p4, layer 4, MIS 3) (WOJTAL 2007; KRAJCARZ & MADEYSKA 2012); the Mamutowa Cave (layer 5, MIS 3) (WOJTAL 2007); the Ciemna Cave (damaged calcaneus, layer C8, MIS 5) (KRUKOWSKI 1939-1948; MARCISZAK et al. 2017). The single mts II from layer 6 of the Borsuka Cave (WILCZYŃSKI et al. 2012a), from the layer 4, cave no. 4 at Birów Hill and trench F of the Kraków Spadzista open-air site (LIPECKI & WOJTAL 2015) are dated at MIS 2. The species is also found in Sudetic caves, where the most spectacular find is a partially preserved skeleton of very large and robust male dated at the postglacial period (MARCISZAK et al. 2016, 2017). Besides, isolated canines from the Północna Duża Cave and from the layer 21 (trench V) of the Niedźwiedzia Cave, as well as a dozen well-preserved long bones and metapodials from the Naciekowa Cave of Late Pleistocene age can be added to the inventory. Likewise, the single premolar from the cave in Czarkowa and the fragment of right mandible with p3-p4 from the Mamutowa Cave, both without a stratigraphic context, are most likely of the Late Pleistocene age. Finally, it can be added that before the World War II a complete left foot of a particularly large individual was found in the archaeological site Gródek 2 in the environs of Równe (now Riwne in Ukraine), which was then a part of Poland (LOTH 1933). It seems that the find from Solna Jama is the only reliable postglacial record of the species from Poland. Till now no wolverine remains were found in any archaeological Holocene site in Poland (WYROST 1994; SOMMER & BENECKE 2004). No remains were found during our detailed revision of the material from most of those localities.

Detailed metric and morphological studies showed that late Early and Middle Pleistocene members of the genus *Meles* did not differ significantly from the modern badger in their teeth structure (MADURELL-MALAPEIRA et al. 2011; MARCISZAK 2012). No differences were found when the material from numerous Late Pleistocene and Holocene sites was compared with stratigraphically older remains. Similarly, no significant differences between skeletal bones were found. Overall, the variation ranges and proportions are com-

parable to those of the modern badger. The observed small differences are probably due to interspecific variations. It should be also noted that the badger regularly disturbs the structure of cave deposits, digging extensive systems of burrows. As a result, its remains found in a layer do not have to be of similar or the same age as the sediments and other relics found in the same horizon (WISZNIOWSKA 1980). Taxonomic and morphometrical analysis of such early finds is in many cases rendered very difficult or even impossible by the fragmentation of the material and the presence of teeth without any significant diagnostic features.

The badger is the most common mustelid in the Late Pleistocene assemblages; it occurred in colder and warmer periods (WOLSAN 1989; SOMMER & BENECKE 2004; WOJTAŁ 2007; MARCISZAK 2012). The badger commonly used caves and rock shelters as a place to rest and raise their young. An example of such behavior is the site Mała Cave (Jura Wieluńska). An abundant material dated as Holocene was found only in the layer 22a-b. The badger burrows' systems were found to reach Pliocene layers (WISZNIOWSKA 1980). The species also plays an active role in the accumulation of debris; its waste products accumulate in its long-term latrines which are parts of underground corridors. Besides, various debris accumulate in the deep corridors, sometimes in considerable quantities. Examples of this kind of accumulation are the German sites Pisede 1 and Pisede 2, where postglacial and Holocene material was excavated from badger burrows (PETERS et al. 1973).

The badger is a highly social animal with a developed social structure and attached to the residence, which many generations may use (for more than 100 years). During that time the whole family can create a system of burrows and corridors of several hundred square metres. The presence of juvenile specimens confirms the use of caves as places to rear offspring (KURTÉN 1965; WISZNIOWSKA 1980; MALLYE 2007; MARCISZAK 2012). Abiotic factors, predators and a man also played a role in the accumulation of badger bones. Numerous archaeological sites were found to hold large accumulations of badger bones material with traces of human activity (LÜPS & WANDELER 1993; CHARLES 2000; MALLYE 2007).

Martes martes and, to a lesser extent, the badger are more or less associated with deciduous forests (SOMMER & BENECKE 2004; WILCZYŃSKI et al. 2012a), but the marten lived also in cooler habitats and taiga-type forests (ANDERSON 1970; HERNÁNDEZ-FERNÁNDEZ 2001; MARCISZAK 2012). The two smallest mustelids, *Mustela erminea* and *Mustela nivalis* are generally regarded as euryoecious, however the stoat usually prefers cooler conditions compared to the least weasel (ABRAMOV & BARYSHNIKOV 2000; KING & POWELL 2007).

Remains of *Lynx lynx* are very rare in the Polish archeological and paleontological sites, almost all of them of postglacial or Holocene age. Among older excavations the species was recorded from mixed Pleistocene-Holocene sediments of the Okiennik shelter (LUBICZ-NIEZABITOWSKI 1938; KRUKOWSKI 1939-1948; KOWALSKI 1951, 1959; STEFANIAK & BIEROŃSKI 2009; STEFANIAK et al. 2009), the Komarowa Cave (NADACHOWSKI et al. 2009), the Magurska Cave (LUBICZ-NIEZABITOWSKI 1938) and the Poszukiwaczy Skarbów Cave (HOYER 1928). However the pre-Neolithic age of those findings seems to be highly questionable (BARYCKA 2008). Also the record from the Koziarnia Cave, based on an isolated canine, was in fact a misidentified *Canis lupus* (BARYCKA 2008). The species was also mentioned from 14 archaeological sites dated at Holocene (WOLSAN 1989; WYROST 1994). Two of them, Zawichost (KRYSIAK 1967a; KRYSIAK & LASOTA 1971) and Kamień

Łukawski were of Neolithic age, while three, Tarławki (LASOTA-MOSKALEWSKA 1979), Smuszewo (GODYNICKI & SOBOCIŃSKI 1977) and Biskupin (LUBICZ-NIEZABITOWSKI 1935-1936, 1938) were dated at 0.7-0.4 ka BP (WYROST 1994). Finally, there are nine records of lynx remains from the Middle Ages: Stare Drawsko and Gdańsk (JAWORSKI 1952; KRYSIAK 1955, 1956, 1967b; SOBOCIŃSKI 1980), Gniezno (SOBOCIŃSKI & SCHRAMM 1972), Kruszwica (SOBOCIŃSKI 1964), Czeladź, Wrocław and Opole (WYROST & CHRZANOWSKA 1985), Radom (KRYSIAK et al. 1975) and Sąsiadka (KRYSIAK 1966). After the end of the 18th century the species almost completely disappeared from the area west of the Vistula river (BIENIEK & WOLSAN 1992).

A nearly complete lynx skeleton was also found in the Wierna Cave in Częstochowa Upland (GAŁUSZKA 1992; STEFANIAK et al. 2009). Holocene remains of the species in the same upland were found in the layer 1-b of the Biśnik Cave (MARCISZAK et al. 2011). The only record of the lynx from Sudetic caves comes from the trench V of the Niedźwiedzia Cave, where a maxilla fragment was found in postglacial/Holocene deposits (MARCISZAK et al. 2016). Pre-MIS 1 occurrences of *Lynx lynx* are even less frequent. Well-preserved lynx remains dated at MIS 3-2 were discovered during the last ten years in sediments of the Ciemna Cave (VALDE-NOWAK et al. 2014; MARCISZAK et al. 2017). Recently, as a result of re-examination of the old material, some isolated teeth and postcranial bones were found in late Middle Pleistocene layers of the Biśnik Cave. However, the material has not been described in detail so far and for now it can only be classified as an undetermined member of the genus *Lynx*.

Felis silvestris is a permanent component of palaeontological assemblages, but usually it is represented by a rather scanty material. Most of the so called “fossil” specimens, whose age was estimated based on biostratigraphical or other indirect evidence, turned out to be postglacial or subfossil. The conjecture was confirmed by a few ¹⁴C AMS dates, which showed a young age of those remains (KRAJCARZ et al. 2015b; MARCISZAK et al. 2017). Except very few bones, most specimens were younger than 12-10 ka. It seems that the earlier literature mentions of Pleistocene occurrence of the species were based on specimens from mixed layers. Examples are the following records: skulls from the Raj Cave (KOWALSKI 1967), a humerus and an ulna from the shelter under Tunel Wielki (NADACHOWSKI 1988), a mandible with a phalanx from the Obłazowa Cave (LIPECKI & WOLSAN 2003), the Ciasna Cave (NADACHOWSKI 1988; NADACHOWSKI et al. 1989), two hemimandibles of the same individual from the Maszycka Cave (OSSOWSKI 1883; KOWALSKI 1951), a humerus from the Mamutowa Cave (NADACHOWSKI et al. 1989) and a calvarium, few mandibles and long bones from Zbójecka, Krakowska and Nietoperzowa caves (RÖMER 1883).

The species was also quite common in Sudetic caves. ZOTZ (1939) mentioned an unidentified cat from the deposits of the Obok Wschodniej Cave. The wildcat was identified based on a few isolated teeth and post-cranial bones from the Holocene layers of rock shelters Małgorzata and Trwoga Paleontologa (BIEROŃSKI et al. 2007), as well as the postglacial/Holocene layers of the Solna Jama cave and Niedźwiedzia Cave (MARCISZAK et al. 2015, 2016, 2017). Regarding the record from the Radochowska Cave, it is not even clear if it was the wildcat or domestic cat, because the identification was based on a femur (FRENZEL 1936). The bone was found in the surface strata of the sediments and was not fossilised. *F. silvestris* is very rarely found in Pleistocene deposits of Central Europe (BARYCKA 2008). So far wildcat remains of truly late Middle and Late Pleistocene age are known i.a. from

different layers of the Biśnik Cave (MARCISZAK et al. 2011) and the Nietoperzowa Cave (KOWALSKI 1961; BARYCKA 2008).

Both cats, the lynx and the wildcat are relatively rare in cave deposits, which is typical of most medium and small cats. These forms, unlike e.g. leopard, rarely use caves as shelters to raise cubs. Small cats are solitary, shy, elusive hunters which usually avoid any competition with similar sized and larger carnivores such as wolves or wolverines, which is probably one of the major reasons for their rarity in cave sediments. The scarcity of their remains in cave deposits is due to poor penetration by these predators inside and around the caves. Due to their anatomy (a movable spine, very flexible limb joints, retractable claws) cats are able to survive a fall even from a high altitude and escape from caves which are a kind of trap such as karstic sinkholes. Because of their solitary, secretive lifestyle and relatively large territories, they were only occasional human victims, although their fur was (and is) regarded as valuable (BARYCKA 2008; MARCISZAK et al. 2011).

V. CONCLUSIONS

Twelve carnivore species documented the deposition in the Borsuka Cave during the last 27 ka. The carnivores from the Borsuka Cave form two different assemblages. The younger one, from Holocene layers I-IV, is dominated by remains of *Vulpes vulpes*, *Meles meles*, and *Felis silvestris*, with admixture of the less frequent *Ursus arctos arctos*, *Martes martes* and *Mustela ex. gr. eversmanni-putorius*. The older assemblage from layers V-VII, dated as MIS 2, is a mixture of species adapted to cold climate and steppe-tundra and/or tundra-open boreal forests (*Vulpes lagopus*, *Gulo gulo*, *Mustela erminea*), euryoecious forms (*Canis lupus*, *Mustela nivalis*, *Ursus arctos arctos*) and forest-dwellers (*Martes martes* and *Lynx lynx*).

Detailed morphometrical analyses show that many forms were associated with cold periods and cool climate conditions. The large size of *Gulo gulo* and *Martes martes* as well as the notably small dimensions of *Mustela erminea* and *Mustela nivalis* provide good examples. Likewise, the large size of the brown bear, despite the already simplified teeth morphology characteristic of *Ursus arctos arctos*, may reflect colder climate conditions.

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