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Ursus arctos L., 1758 from Bukovynka Cave (W Ukraine) in an overview on the fossil brown bears size variability based on cranial material

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ABSTRACT

Brown bear *Ursus arctos* is a permanent member of European Middle and Late Pleistocene carnivore assemblages, which shows great body size fluctuation over time. To study this subject we carried out extensive comparison of 37 cranial metric features based on 2954 measurements coming from 263 specimens. In the statistical analyses we included a new complete brown bear calvarium which was found in Bukovynka Cave in Ukraine and dated to postglacial period. The cranial material was divided into male and female sets and classified according to geographic and stratigraphic affiliation of the samples. Analyses revealed clear decrease in many skull dimensions from the Middle Pleistocene specimens through the Late Pleistocene and postglacial to the Holocene skulls. The trend is probably related with general climatic changes during this period. However, Late Pleistocene specimens from Iberian Peninsula were significantly smaller from other Late Pleistocene European skulls or even a bit younger from the Late Glacial and postglacial period for some dimensions. The deviation from the global trend could result from their isolation from other European populations. These conclusions can be drawn both for male and female skulls. The decrease in body size showed that *U. arctos* is dynamically evolving species. Thus, the size does not seem to be a perfect criterion in determining the biochronological age of the brown bear findings although a general decreasing trend in size with time is clearly visible. The size of brown bear is under the influence of many factors such as great sexual dimorphism, individual and population variability as well as global and local climatic conditions.

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1. Introduction

Brown bear (*Ursus arctos*) is a permanent member of European carnivore assemblages since the latest part of the Early Pleistocene (Baryshnikov, 2007; Rabeder et al., 2009). Opposite to *U. arctos*, bears from spelenoid lineage (so called *Ursus* ex. gr. *spelaeus*) are the most numerous large mammal species in cave sediments (Baryshnikov, 2007). The impressive posture, great size of the brown bear and fact, that it constituted a real threat to *Homo sapiens*, made that this species have fascinated humans since prehistoric times (Kurtén, 1968a). Some authors (Zotz, 1937a, 1937b, 1939, 1951) pointed even a bear worship, however, the samples were most probably naturally worn rather than processed by human (Wiśniewski et al., 2009).

U. arctos is characterized by great size variation through its whole time span. Most authors reported the decreasing size process in the brown bear lineage evolution in the end of the Late Pleistocene and beginning of the Holocene and simultaneously accented particularly large size of fossil brown bears (Ball, 1850; Adams, 1880, 1883; Reynolds, 1906; Couturier, 1948; Erdbrink, 1953; Thenius, 1956; Kurtén, 1959, 1964, 1965, 1968b; Bonifay, 1971; Kurtén, 1977, 1978; Pohar, 1981; Ballesio, 1983; Torres Pérez Hidalgo, 1988a, 1988f; Sabol, 2001a; Baryshnikov and Boeskorov, 2004; Baryshnikov, 2007; Pacher, 2007; Rosendahl and Döppes, 2011). Here we carried out extensive comparison of large series of geographically and stratigraphically diverse samples of brown bears from Eurasia in the context of size changes. In the studied set we also included the newly found in Bukovynka Cave (Ukraine) intact skull of *U. arctos*, which was described here for the first time. The earliest occurrence of brown bear in Ukraine was documented

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from few late Middle Pleistocene sites. This species is also known from many Late Pleistocene localities (Krakhmalnaya, 1999 and references therein; Ridush, 2009). In the territory of Ukraine brown bear was widely distributed, but not abundant. The number of localities and individuals are larger in postglacial and Holocene sites, in which brown bear bones constituted up to 2% of skeleton remains of hunted animals (see Krakhmalnaya, 1999 and reference therein), e.g. in Lesnik Cave on Ai-Petri plateau (Crimea), dated to 10,155 ± 40 BP. In Holocene *U. arctos* is found across most of Europe (Baryshnikov, 2007; Pacher, 2007) and until historical times its geographical range covered almost the whole Ukraine territory (Krakhmalnaya, 1999). However, recently it is restricted only to Carpathian Mountains in the west Ukraine, while European large, stabile populations can be found in central and eastern part of the continent (Krakhmalnaya, 1999). Few survived small, isolated populations in Western Europe are highly threatened (Jakubiec, 1993; Baryshnikov, 2007) (Fig. 1).

2. Material and methods

2.1. Locality

Bukovynka Cave (48°18′07″N 26°32′57″E) is located 1.5 km to the North West from Stalnivtsi village of Novoselytsya district, Chernivtsi region (northern Bukovyna) (Fig. 1). Since 1976, the cave was explored by speleologists, while paleontological and paleogeographical studies started in 1998. Previously published papers only briefly mentioned the general description of the site and some paleontological finds (Ridush, 2009). The site is the second largest Bukovynian cave, with the total length of corridors of 5155 m. It is developed in the inactive gypsum quarry, and the three artificial entrances are situated ca. 135 m a. s. l. The cave is a maze type, with three main levels. The lower floor is constructed by narrow galleries with rounded vaults, partially filled with clays and loams. The middle (main) level is represented by series of subparallel galleries, connected by narrow corridors. The upper floor is created by narrow fissures of corrosive origin, connected with the middle level by vertical pits (Bondar and Ridush, 2014).

Analyzes of the deposits showed, that the sediments represent three main types: fluvial, allochthonous and aeolian. Only the allochthonous sediments contained the paleontological finds. Three trenches have been made: two in Trapeznyi Chamber (Sections 1 and 2), and one in Dry Chamber (Section 3). Sediments in Trapeznyi Chamber are created by light-brown loams in the upper part, gray sandy lays in the middle part and gravel-pebbles and bedrocks in the bottom. The faunal assemblage is strongly dominated by a cave bear *U.* ex. gr. *spelaeus* and is dated to MIS 3–2 (the C^{14} date of a hyena tooth is 41,300 + 1300/−1100 BP, VERA-2529) (Ridush, 2009). Apart cave bear, also red fox (*Vulpes vulpes*), cave hyena (*Crocuta crocuta spelaea*), horse (*Equus caballus*), wooly rhino (*Coleodonta antiquitatis*), wild boar (*Sus scrofa*), giant deer (*Megaceros giganteus*) and steppe bison (*Bison priscus*) have been found. Crashed bones with hyena activity and the presence of hyena coprolites and juvenile individuals suggested that this site could be a Late Pleistocene hyena den (Ridush, 1998, 1999, 2009). However, bone consumption by other carnivores, e.g. bear or wolf, cannot be also excluded (Fourvel, 2012; Fourvel et al., 2014).

The studied here brown bear skull (Fig. 2) has been found in the lowermost part of Section 3 in Dry Chamber, in the layer S17b at depth 224–226 cm in pale-grey loams without layers and inclusions. The whole profile from Section 3 was divided into 18 main layers (some with two sub-layers), 250 cm thick. The sediments

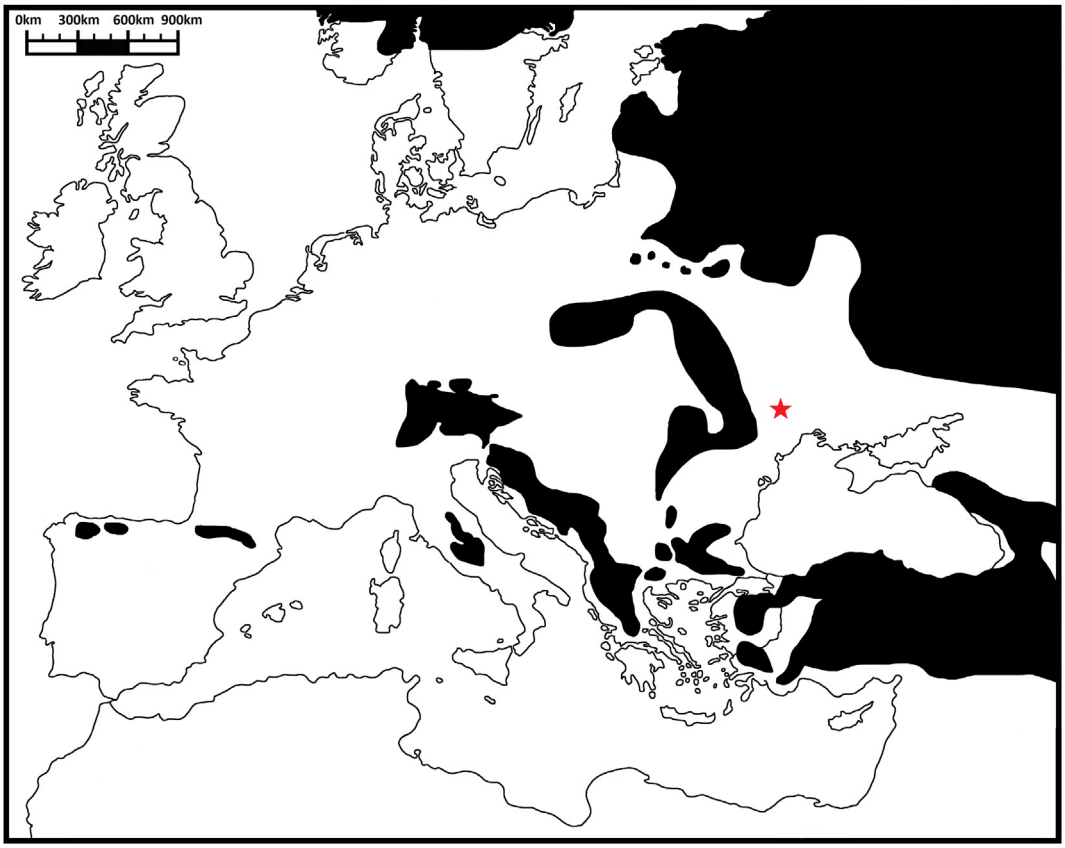

Fig. 1. Localization of Bukovynka Cave (red star) and the recent range of distribution (black area) of the brown bear *U. arctos* in Europe (adapted and changed from http://maps.iucnredlist.org/map.html?id=41688). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

consist of loams, light brown in upper part, darkening from the top to the bottom. Section 3 corresponds to MIS 1 and included the brown bear skull found at the bottom and dated to 10,730 ± 60 C^{14} yr BP (Poz-46240), which gives median calibrated age 12,674 with 95.4% interval 12,735–12,575 yr BP based on OxCal 4.2.3 (Bronk Ramsey and Lee, 2013). The top of the section was dated to unit S1 with the age 1000 BP. Apart the bear skull, the only other finding is a well preserved cranium of bobac (*Marmota bobac*) with some postcranial elements, found in layer S13, at depth 110 cm (Bondar and Ridush, 2014).

2.2. Material

The examined cranium from the Bukovynka Cave (Fig. 2), kept in the collection of the Department of Physical Geography and Natural Management, Chernivtsi "Fed'kovych" National University in Ukraine, was compared with European *U. arctos* skull series (see Supplementary material, Tables S1 and S2 as well as Tables 1 and 2 with summary statistics). For each calvarium, basic information (detailed locality, stratigraphical age, sex and main references) has been given. In the morphological and metrical features only complete calvarii have been used. We considered in total 2954 measurements from 263 specimens. Osteological terminology and measurements of teeth and cranium follow Argant (2010). We compared 37 cranial metric features denoted briefly by c for cranium and m for maxilla with corresponding numbers (see Fig. 3): c1-total length (prosthion–acrocranion), c2-condylobasal length (prostion-occipital condyles), c3-basal length (prosthion–basion), c4-basicranial length (synsphenion–basion), c5-basifacial length (prosthion–synsphenion), c6-neurocranium length (point F-acrocranion), c7-viscerocranium length (prosthion-point F), c8-facial length (prosthion-point F), c9-nasal length (rhinion–nasion), c10-rostrum length (prosthion-infraorbital), c11-palatal length (prosthion–staphylion), c12-breadth at the processus paraoccipitalis, c13-maximal breadth of occipital condyles, c14-mastoid breadth (otion–otion), c15-breadth of foramen magnum, c16-height of foramen magnum (basion–opisthion), c17-maximal neurocranium breadth (euryon–euryon), c18-breadth at zygomatic arches (zygion–zygion), c19-postorbital least breadth (postorbital bar), c20-frontal breadth (ectorbital–ectorbital), c21-least breadth between orbits (entorbital–entorbital), c22-cranial height (acrocranion–basion), c23-maximal cranial height (staphylion-frontal), c26-maxilla breadth at nasal aperture, c27-least breadth between infraorbital foramens; m1-upper jaw maximal breadth, m2-upper jaw minimal breadth, m3-maximal breadth at the canine alveoli, m4-maximal breadth at the M2 alveoli, m5-external length C1–M2 (anterior margin of alveole of C1–posterior margin of alveole of M2), m6-internal length C1–M2 (posterior margin of alveole of C1–posterior margin of alveole of M2), m7-upper tooth row length (anterior margin of alveole of P4–posterior margin of alveole of M2), m8-upper molars row length on alveoles (anterior margin of alveole of M1–posterior margin of alveole of M2), m9-diastema length (posterior margin of alveole of C1–anterior margin of alveole of P4). In addition to that, the length of P4 (PM) was also included in the studies.

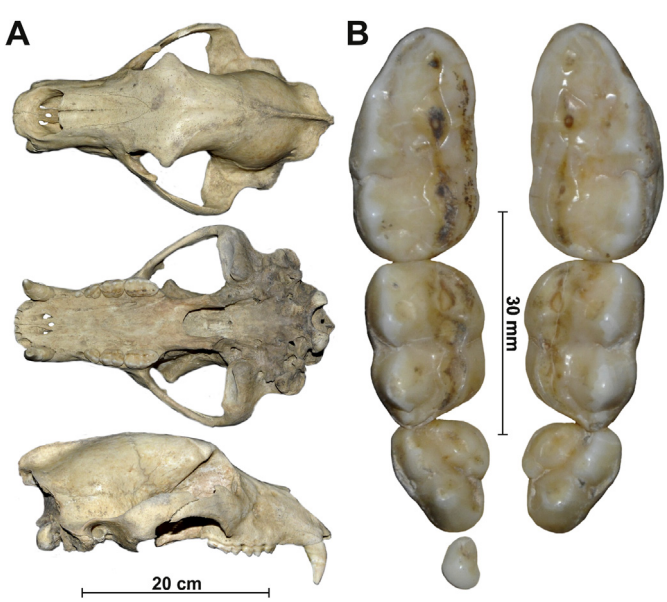

Fig. 2. Calvarium (A) and morphology of upper cheek teeth, P4–M2 (B) of brown bear *Ursus arctos* from Bukovynka Cave.

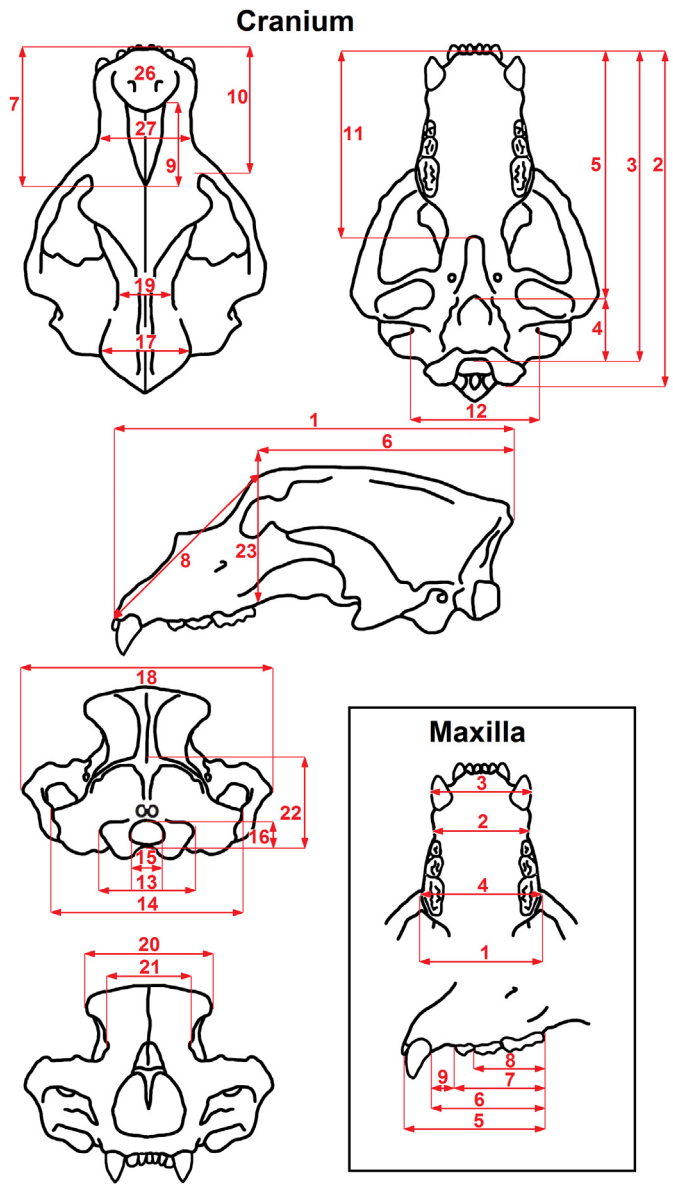

Fig. 3. Scheme of measurements of the bear skull, according to Argant (2010). For details about the measurements see Material section.

Table 1
Summary statistics of cranial (c) and maxilla (m) measurements for male skulls divided in groups according to geographic location and stratigraphic position: mean [minimum–maximum]; sample number. For measurements schema see Fig. 3. PM is the length of P4.

	Middle Pleistocene	Late Middle Pleistocene	Late Pleistocene	Late Pleistocene from Spain	Late Glacial Postglacial	Holocene	Recent
c1	454.1 [431.0–477.0]; 4	412.8 [384.0–442.0]; 5	414.8 [379.2–452.0]; 20	373.9 [338.0–398.6]; 13	374.6 [316.0–416.0]; 15	358.3 [334.0–395.0]; 6	361.2 [321.0–428.0]; 61
c2	423.1 [410.5.0–429.0]; 4	387.5 [377.0–398.0]; 2	391.0 [366.2–416.0]; 11	334.5 [314.0–355.0]; 4	352.3 [313.3–381.0]; 9	327.1 [281.8–370.0]; 6	336.8 [303.0–405.0]; 49
c3	396.4 [386.5–404.0]; 4	355.0; 1	360.2 [322.0–392.0]; 17	322.6 [297.0–347.1]; 11	332.4 [281.0–360.0]; 16	300.0 [245.0–338.0]; 4	322.1 [286.4–380.5]; 17
c4			101.8; 1	114.0 [102.0–121.0]; 4	92.9 [80.0–101.0]; 7	92.1 [78.6–115.3]; 3	87.6; 1
c5			236.4; 1	214.1 [195.0–235.2]; 11	229.7 [201.0–257.0]; 8	191.2 [111.0–261.7]; 5	136.4 [108.0–220.2]; 6
c6	239.6 [227.0–255.0]; 4	228.9 [215.0–242.0]; 4	224.5 [180.0–247.4]; 10		223.5 [200.0–241.0]; 5	194.0 [180.0–206.1]; 4	209.1; 1
c7	225.0 [223.2–229.0]; 4	177.5 [160.0–201.0]; 4	188.1 [150.0–220.0]; 10	183.0 [176.0–190.0]; 2	167.3 [152.0–185.0]; 6	161.5 [156.0–167.0]; 2	123.6; 1
c8						186.0; 1	152.1; 1
c9			80.0; 1	105.1 [91.5–114.0]; 7	93.8 [84.0–105.0]; 5		84.6; 1
c10	172.5 [171.3–174.0]; 3	147.0 [135.0–159.0]; 2	147.0 [133.0–165.0]; 6	152.3 [125.8–167.0]; 9	144.3 [126.0–156.0]; 15	127.8 [127.5–128.0]; 2	135.2 [127.0–148.0]; 15
c11	231.2 [224.5–239.0]; 4	204.3 [198.5–210.0]; 2	201.7 [173.0–230.0]; 15	183.8 [172.0–196.3]; 11	182.3 [160.0–197.0]; 10	176.2 [139.5–205.0]; 5	179.6 [163.2–208.0]; 9
c12			123.9 [121.2–131.0]; 4		157.5 [150.0–165.0]; 2	136.0; 1	116.8; 1
c13	85.1 [78.0–90.0]; 4	83.7 [82.3–85.0]; 2	82.7 [71.0–96.0]; 14	69.2 [63.6–73.1]; 11	73.1 [59.8–88.0]; 13	63.3 [55.5–68.9]; 3	71.3 [63.0–84.0]; 10
c14	204.3 [185.0–221.5]; 4	224.9 [219.0–230.8]; 2	190.4 [156.0–220.4]; 14	172.4 [144.0–189.0]; 12	171.6 [135.0–212.0]; 19	153.4 [133.6–165]; 5	119.7 [96.0–172.3]; 20
c16			28.0; 1				31.4 [20.2–36.5]; 4
c17	117.0 [105.0–129.5]; 4	114.0; 1	115.2 [107.0–138.0]; 10		105.8 [101.0–110.0]; 4	91.6 [68.0–111.4]; 4	87.8 [81.2–95.6]; 6
c18	270.0 [246.0–300.0]; 3	251.8 [251.5–252.0]; 2	234.9 [200.0–268.8]; 9	235.8 [198.0–268.6]; 10	227.2 [195.0–275.0]; 16	209.7 [186.8–235.0]; 7	211.5 [171.0–253.0]; 60
c19	79.6 [75.0–84.5]; 4	82.5 [82.0–83.0]; 2	84.1 [63.2–108.0]; 12	79.6 [72.0–84.0]; 10	79.7 [67.7–94.0]; 14	78.9 [76.0–82.4]; 3	73.4; 1
c20		91.0; 1	97.1 [82.0–126.9]; 5	121.3 [79.0–140.4]; 11	123.5 [101.0–150.0]; 21	97.9 [62.1–120.0]; 7	81.6 [62.1–126.0]; 64
c21	89.3 [84.0–93.2]; 4	105.1 [89.5–135.0]; 3	105.1 [82.4–147.0]; 9	92.0 [78.0–112.8]; 11	85.9 [72.0–114.0]; 21	77.4 [74.0–80.7]; 2	78.9 [71.0–86.5]; 4
c22	129.9 [120.0–139.4]; 3	125.8 [118.5–133.0]; 2	107.1 [83.0–133.0]; 12	95.3 [88.0–103.0]; 4	98.6 [72.0–117.5]; 14	80.2 [68.8–89.5]; 3	77.6 [63.0–109.0]; 47
c23			130.0 [96.0–159.0]; 3		101.9 [83.0–116.0]; 9		93.5 [85.8–109.0]; 18
c24		45.0; 1	59.5 [56.0–63.0]; 2				
c28						71.1 [69.5–72.6]; 2	61.5 [56.0–72.0]; 5
m1	102.6 [96.0–107.0]; 3	95.5; 1	99.4 [89.0–108.8]; 8		93.0 [84.0–98.0]; 3	77.5; 1	87.2; 1
m2	105.3 [101.5–109.0]; 2	103.9 [99.0–114.7]; 4	93.7 [80.0–107.3]; 2	93.0 [82.0–104.0]; 4	95.6 [83.0–110.0]; 9	98.3 [91.0–105.5]; 2	57.5 [50.0–64.0]; 6
m3		85.0; 1	48.0; 1	65.6 [56.0–72.5]; 10	75.2 [52.5–100.0]; 14	75.5; 1	77.7 [66.2–91.0]; 45
m4	96.0; 1	93.8 [80.0–99.5]; 4	84.5 [60.9–101.0]; 8	87.1 [80.0–95.0]; 4	83.4 [75.0–92.0]; 12	82.7 [78.0–87.4]; 2	52.5; 1
m5	104.4 [98.0–109.0]; 4	142.2; 1	106.7 [57.0–176.0]; 9	83.1 [55.6–104.0]; 9	69.9 [62.5–81.5]; 5	91.2; 1	122.8 [122.0–123.5]; 3
m6	157.2 [154.0–159.5]; 4	106.1 [80.8–146.1]; 3	138.5 [97.0–161.0]; 6	130.5 [121.0–139.0]; 4	141.5 [127.0–164.0]; 8	95.5; 1	98.4; 1
m7		148.0; 1	131.5 [80.8–162.5]; 7	108.7 [100.0–115.8]; 11	105.7 [84.0–114.0]; 10	93.5; 1	73.6 [67.0–89.0]; 18
m8	89.5 [85.0–95.0]; 4	81.5 [80.0–83.0]; 2	84.7 [75.8–93.8]; 10	73.8 [68.0–78.6]; 13	75.7 [65.0–87.0]; 14	84.5 [73.4–95.5]; 2	56.0; 1
m9		14.0; 1	32.1 [28.0–37.0]; 6		31.9 [26.0–40.0]; 8		29.6 [18.5–38.5]; 19
PM		60.3 [57.0–63.5]; 2		59.8 [52.5–81.0]; 13	60.0 [54.0–66.0]; 6	57.1 [53.0–61.2]; 2	

Table 2
Summary statistics of cranial (c) and maxilla (m) measurements for female skulls divided in groups according to geographic location and stratigraphic position: mean [minimum–maximum]; sample number. For measurements schema see Fig. 3. PM is the length of P4.

	Late Pleistocene	Late Pleistocene from Spain	Late glacial postglacial	Holocene	Recent
c1	348.5 [321.0–371.9]; 5	310.0 [272.0–340.0]; 14	327.6 [321.5–339.0]; 3	308.1 [285.0–335.0]; 14	295.7 [209.1–355.0]; 68
c2	330.4 [314.2–351.7]; 5	287.0 [271.0–303.0]; 4	299.0 [298.9–299.0]; 3	297.4 [275.0–320.0]; 11	276.5 [196.4–335.0]; 53
c3	308.2 [294.4–325.5]; 5	277.7 [257.0–309.2]; 12	289.0 [283.0–295.5]; 3	273.3 [258.4–298.0]; 6	265.2 [195.0–302.0]; 36
c4	91.5 [75.0–108.0]; 2	95.3 [93.0–98.0]; 3	78.4 [77.0–80.0]; 3	67.8 [60.4–72.4]; 6	71.6 [52.0–82.0]; 18
c5	258.0; 1	181.7 [168.0–201.0]; 12	208.6 [208.1–209.0]; 2	178.4 [170.1–184.9]; 5	160.4 [73.9–222.0]; 26
c6	210.5 [189.5–231.5]; 2	172.0 [168.0–176.0]; 2	178.6 [170.0–183.7]; 3		172.7 [137.0–199.0]; 20
c7	177.9 [176.0–179.8]; 2	129.8 [122.5–141.0]; 3	156.2 [152.0–161.0]; 3		128.2 [94.0–147.0]; 23
c9	83.3 [79.0–87.5]; 2	79.2 [74.0–86.7]; 10	87.8 [84.5–91.0]; 2		72.5 [51.0–90.0]; 21
c10	133.0 [130.3–135.6]; 2	136.4 [124.0–148.0]; 11	125.2 [120.0–128.0]; 3		113.9 [68.0–132.6]; 41
c11	161.5 [101.0–180.6]; 5	158.3 [146.5–173.0]; 14	163.3; 1	152.2 [138.4–168.0]; 9	145.9 [107.7–168.0]; 33
c13	71.4 [69.4–72.4]; 4	59.9 [50.3–71.0]; 12	65.2 [60.3–71.0]; 4		56.9 [46.4–66.0]; 5
c14	157.5 [140.0–179.7]; 5	137.2 [124.0–165.0]; 13	146.4 [140.5–156.0]; 4	126.3 [122.0–130.2]; 3	112.0 [83.3–145.0]; 45
c15	33.1 [32.0–34.1]; 2	30.9 [24.0–34.5]; 11	29.9 [27.9–31.7]; 3		
c16	21.5 [20.0–23.0]; 2		19.6; 1		33.0; 1
c17	103.7 [103.1–104.2]; 2		104.9 [104.0–105.6]; 3		72.7 [59.2–94.4]; 7
c18	195.3 [182–211.7]; 4	188.4 [157.0–219.4]; 12	196.1 [184.0–203.0]; 4	192.1 [180.0–208.5]; 6	167.5 [113.8–204.0]; 74
c19	72.5 [68.5–76.7]; 5	70.8 [64.0–76.5]; 13	83.3 [70.0–111.5]; 4	77.0 [55.9–107.2]; 13	69.5 [58.0–80.0]; 46
c20	105.6 [99.0–112.0]; 3	96.2 [71.0–113.0]; 14	102.8 [99.5–105.0]; 3	94.9 [78.4–112.5]; 7	82.3 [61.0–102.5]; 55
c21	73.7 [68.7–84.2]; 4	75.5 [64.3–90.0]; 13	74.3 [71.0–77.6]; 4		64.1 [45.0–79.0]; 52
c22	90.7 [70.0–111.7]; 4	75.5 [75.0–76.0]; 2	87.1 [81.0–94.4]; 4		75.9 [45.6–93.0]; 29
c23	130.0; 1		92.4; 1		80.3 [62.0–96.0]; 42
m1	78.6 [76.9–80.3]; 2		80.5 [71.4–87.1]; 3		
m2	102.0; 1	79.0 [78.0–80.0]; 2	85.5 [85.0–86.0]; 2		71.1 [41.0–84.0]; 32
m3		53.4 [37.3–62.4]; 14	59.7 [51.0–68.4]; 2		64.1 [50.0–77.0]; 50
m4	76.7 [76.3–77.0]; 3	76.1 [69.0–88.3]; 3	75.4 [71.5–83.0]; 4		63.8 [47.0–74.0]; 24
m5	89.9 [89.3–90.5]; 2	82.4 [78.0–88.0]; 11	89.3 [61.0–121.0]; 3	78.8 [69.6–87.2]; 8	105.6 [93.0–112.0]; 7
m6	126.8 [120.0–134.0]; 4	105.5 [86.5–117.0]; 3	121.9 [121.7–122.0]; 2		129.1; 1
m7	110.0; 1	94.6 [68.7–107.3]; 14	94.6; 1		81.7 [62.7–101.0]; 43
m8	75.0 [67.2–85.0]; 5	67.8 [53.4–74]; 14	75.3 [70.9–82.0]; 3	67.5 [62.4–71.1]; 7	67.7 [62.0–78.0]; 21
m9			23.7; 1	40.5; 1	22.3 [14.5–35.0]; 43
PM		54.6 [47.9–59.5]; 13	57.5 [57.0–58.5]; 3		

All crania were divided into several groups according to their sex, geographic locality and stratigraphic position. Male and female skulls were divided into groups: Late Pleistocene, Late Glacial–Postglacial (LGP) and Holocene (H). The Late Pleistocene group was considered both as the whole set and divided into skulls from Spain (LPS) and the rest European sites (LP). The separation of this group is justified by results of other researches who reported that the Late Pleistocene skulls from Spanish show relatively smaller dimensions in comparison to other European crania. The separation of other geographical groups was not possible because of their poor sampling. In the case of male skulls, Middle Pleistocene (MP) and Late Middle Pleistocene (LMP) sets were also created. Moreover, recent European brown bear skulls (R) were used for comparison (data from Schäff, 1889; Jakubiec, 1993; Østbye et al., 2006 and own measurements).

2.3. Methods

Measurements of the skull from Bukovynka Cave (Fig. 3) were taken with an electronic caliper, to the nearest 0.1 mm; each value given here is the mean of three measurements. All dimensions are given in mm. Teeth terminology and morphotypes are according to Rabeder et al. (2009). Chronostratigraphy is based on Lisiecki and Raymo (2005).

Statistical analyses were carried out in R package (R Core Team, 2014, R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, http://www.R-project.org) on sets containing at least three samples. In order to check if the studied variables fulfil the normal distribution, which is an underlying assumption of parametric tests, we applied the Shapiro–Wilk test, regarded as the most powerful normality test (Razali and Wah, 2011). The second assumption of parametric Analysis of Variance (ANOVA), the homogeneity of variance across studied groups was checked with the more robust version of Lévene's test using the group medians. When the assumptions about normality and variance were fulfilled the parametric one-way ANOVA with Tukey HSD post-hoc test was applied in the case of more than two groups' comparison. The Tukey test was selected because it is the most appropriate in comparison of pairs of means and is moderately conserved. When at least one of these assumptions was violated, the non-parametric counterpart of ANOVA, Kruskal–Wallis test with unpaired Wilcoxon–Mann–Whitney post-hoc test was used in pairwise comparisons between groups. To control the false discovery rate in this post-hoc test, a powerful approach to multiple testing, the Benjamini-Hochberg method for p-value correction was applied (Benjamini and Hochberg, 1995). In comparison of two groups, unpaired t-Student and its non-parametric counterpart unpaired Wilcoxon–Mann–Whitney tests were applied, respectively. Significance of differences was considered with $p < 0.05$ but levels lower than 0.01 and 0.001 were also indicated in the pairwise comparisons in Table 3.

Table 3
Cranial (c) and maxilla (m) measurements for groups of male (lower left triangle) and female (upper right triangle) skulls that statistically significantly differentiated groups: Middle Pleistocene (MP), Late Middle Pleistocene (LMP), Late Pleistocene from Spain (LPS), Late Pleistocene from other European sites (LP), Late Glacial–Postglacial (LGP), Holocene (H) and Recent (R). For measurements schema see Fig. 3. Metric features in normal fonts indicate significance level $p < 0.05$, bold fonts $p < 0.01$ and underlined bold $p < 0.001$.

	MP	LMP	LP	LPS	LGP	H	R
MP		NA	NA	NA	NA	NA	NA
LMP	**c7**, m6		NA	NA	NA	NA	NA
LP	c1, c2, c7, c10, **c11**			c1, c2, c3, c13		c1, **c2**, c3	**c1**, **c2**, **c3**, **c13**, **c14**, c18, c20.m4
LPS	**c1**, c2, **c3**, c10, **c11**, **c13**, c14, m8	c1	**c1**, **c2**, **c3**, c11, **c13**, c14, m7, **m8**		c4, c10	**c4**	**c4**, c9, **c10**, **c14**, c18, **c20**, **c21**, **m3**, m4, **m5**, **m7**
LGP	**c1**, **c2**, **c3**, **c7**, c10, **c11**, c13, c14, c18, c22, m8	c1	**c1**, **c2**, c3.c11, **c13**, c14, c17, c20, c21, m7, m8	c4			c1, c7, **c14**, **c17**, c18, c20, **m4**
H	**c1**, c2, **c3**, **c6**, **c11**, **c13**, c14, **c18**	**c1**, c6	**c1**, **c2**, **c3**, c6, c11, **c13**, **c14**, c17, c22	c20	c20		c2, c18, **m5**
R	**c1**, **c2**, **c3**, c10, **c11**, **c13**, **c14**, c17, **c18**, c22	**c1**, **m2**	**c1**, **c2**, **c3**, **c11**, **c13**, **c14**, **c17**, c18, c20, c21, **c22**, **m7**	c5, c10, **c14**, c18, **c20**, c22, **m2**, **m3**, **m7**	c5, c10, **c14**, c17, **c20**, **c22**, **m2**, **m7**	c14	

Spearman correlation coefficient and their significance were calculated for particular cranial or maxilla measurements ordered based on stratigraphic affiliation of male and female crania, separately. Sets representing by at least three chronological groups were included and the Late Pleistocene group was considered as the whole set in this study.

Hierarchical clustering of different skull groups based on minimum–maximum normalized averages of various measures was performed using *pvclust* function assuming commonly used Euclidean distance and UPGMA (Unweighted Pair Group Method with Arithmetic Mean) as agglomeration method. For assessing the uncertainty in the hierarchical clustering, two types of *p*-values: AU (Approximately Unbiased) *p*-value and BP (Bootstrap Probability) value were computed for each cluster with bootstrap resampling assuming 1000 replications. The AU *p*-value, which is computed by multiscale bootstrap resampling, is considered a better approximation to unbiased *p*-value than the standard BP value computed by normal bootstrap resampling (Shimodaira, 2004).

3. Results

3.1. Taxonomic and morphometric analyses of skull from Bukovynka Cave

The examined material is an intact skull of brown bear *U. arctos*, lacking the mandible and containing C1 and P3–M2 on the left side and C1 with P4–M2 on the right side (Fig. 2). Some shallow, minor marks and scratches on the sagittal crest and neurocranium are visible, but none of the injuries seems to have been the reason for the bear's death. Morphology of the dentition of the specimen matches well brown bear features (Figs. 2B and 4). P1 is not present, whereas left P3 has been preserved but is strongly reduced and single-rooted. Triangular P4 shows simple morphology without cusples like protoloph and metaconulus. The buccal margin of the tooth is almost straight, whereas lingual, as well as anterior and posterior margins are strongly rounded. Paracone is large, round and quite low, metacone is almost equal in size, but lower, and more oval in shape, the valley between the paracone and metacone is strongly pronounced. Elongated and oval low protocone is well developed, and sharply delineated from the remaining part of the crown. Its anterior margin forms a wide, open angle with the posterior margin of paracone. Cingulum is weakly developed, but stronger (creates a small crest) in posterio-buccal part of the crown. It represents morphotype A (according to Rabeder et al., 2009), typical of brown bear.

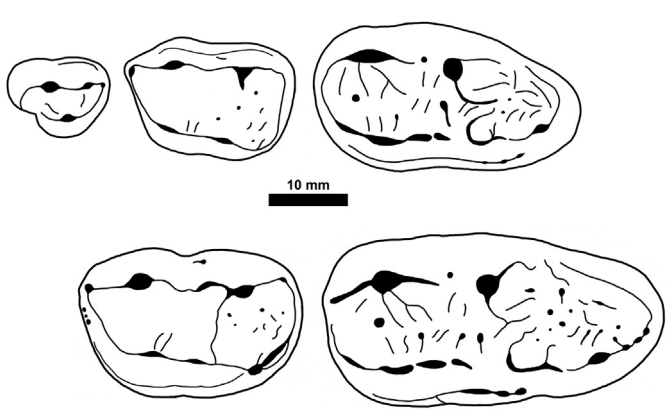

Fig. 4. Morphology of upper check teeth (P4–M2) of brown bear *Ursus arctos*: 1-Late Pleistocene *Ursus arctos priscus* from Winden (according to Rabeder et al., 2009), 2-postglacial *Ursus arctos* from Bukovynka Cave.

Quadratic M1 is symmetrical in occlusal view. Its both margins, buccal and lingual are similar in shape, while posterior part of the crown is rather straight. Small, low and triangular parastyle, is well distinguished from the paracone and is clearly associated with the anterior cingulum. Paracone and metacone are rounded, high and almost equal in size, the valley that separates them is deep. They are well separated from the buccal cingulum. Reduced metastyle is shallow, and elongated, without any posterior edge and is strongly associated with the posterior cingulum. Small, smooth parastyle is weakly developed and its interior crest does not form any cusp in the posterior part. Shallow, small metastyle is also weakly developed, and mesocone is absent. Interior surface of the crown is shallow. Talon surface is smooth, with delicate and thin enamel lines. It is also weakly separated from the poorly developed posterior cingulum. Cingulum crest around the crown is almost absent. Morphotype classifications of M1 dental features are: paracone-0, metacone-0, parastyle and metastyle-small, mesocone-undivided, protocone-inner flange-C2, talonfield-A, lingual cingulum-2.0.

Elongated M2 has all main cusps connected by a crest, which runs by almost whole crown length and follows the tooth outline. Rounded, high paracone is placed far from the metacone and separated from it by shallow, but distinctive valley. Interior surface of the paracone does not have any lines and grooves. Smooth and oval metacone has a centrally placed top. Parastyle, metastyle and posthypocone are absent. Smaller, internal cusps, i.e. protocone, mesocone and hypocone, are smooth cusples weakly developed and poorly distinguishing from the internal crest. Metalophe is flat, without any additional cusps between protocone and metacone. There are also no tracks of any structures between hypocone and

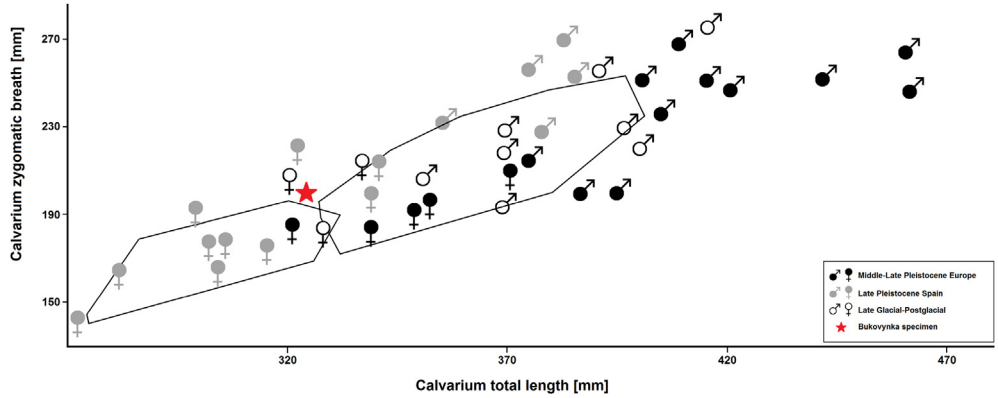

Fig. 5. Total skull length and zygomatic breadth scatter plot of the Pleistocene and Holocene European brown bear *Ursus arctos*. For measurements schema see Fig. 3.

buccal margin. Posterolophe is rather flat. Mesostyle complex is smooth and simply build. Interior slope of protocone is smooth, without any structures. Cingulum is poorly developed, in posterior part is shallow and smooth, better developed only in anterio-lingual part, between protocone and hypocone. In general, the occlusal view of lingual margin is almost straight, while buccal margin is strongly curved in the posterior part. Morphotype classifications of M2 dental features are: parastyle-A1, mesostyle-0, paracone pillar-B, metaloph-B, posterloph-2.0, talon field-B, metastyle-0, posthypocone-1, distal cingulum-A/B, internal slope of protocone-1, lingual cingulum-2.

Morphology and measurements of the specimen indicate that it represents an adult moderate-sized female. Long and well developed sagittal crest fully fused all sutures and epiphysis. Teeth are not very worn, which suggests an adult animal, ca. 5–7 years old. In brown bear sexual dimorphism is strongly pronounced: males are much larger and heavier than females. Also skulls and postcranial bones in the cases of adult males are longer and more robust. The examined specimen is not very large in size. Its total skull length, 322.2 mm, falls exactly between ranges of both sexes of modern Carpathian bears, although it is closer to the mean of males skulls: east and south Carpathian bear ♂♂ = 326.4 mm (260.0–366.0 mm, $n = 77$), ♀♀ = 283.4 mm (240.0–335.0 mm, $n = 39$), west Carpathian bear ♂♂ = 323.5 mm (290.0–339.0 mm, $n = 24$), ♀♀ = 276.5 mm (269.0–284.0 mm, $n = 2$) (Jakubiec, 1993). However, small males and large females can be distinguished using cranium morphology: female skulls are less robust, with less convex forehead, narrower spaced zygomatic arches, less developed crests and neurocranium grooves as well as narrower stout (Jakubiec, 1993; Baryshnikov, 2007). All these features are well marked in Bukovynka specimen indicating that it was a female. Only the zygomatic arches are quite wide (zygomatic breadth = 198.4 mm), but lies still in female size range of east and south Carpathian bear: ♂♂ = 203.2 mm (155.0–253.0 mm, $n = 77$), ♀♀ = 171.6 mm (133.0–203.0 mm, $n = 39$), west Carpathian bear ♂♂ = 213.1 mm (165.0–231.0 mm, $n = 24$), ♀♀ = 171.5 mm (161.0–182.0 mm, $n = 2$) (Jakubiec, 1993). A scatter plot of the total calvarium length and zygomatic arches breadth shows, that in overall Bukovynka skull matches well Pleistocene and Late glacial and postglacial female individuals and simultaneously falls exactly between the ranges of both sexes of modern Carpathian brown bears (Fig. 5). Similar data have been obtained for the total skull length and mastoid breadth ratio (Fig. 6). Crégut et al. (2001) found, that the sagittal crest length can also be regard as a reliable standard for distinguishing sex of brown bear skulls. The length of the crest in female skulls from mid Holocene Mont Ventoux in French varies between 40.0 mm and 97.8 mm ($n = 5$) whereas in male skulls it is from 105.9 mm up to 132.0 mm ($n = 3$). This feature was also found to be statistically reliable for sex distinction in modern Romanian brown bears, because the sagittal crest of males is on average ($L = 111.0$ mm, 66.0–166.0 mm, $n = 38$) much longer than in females ($L = 60.0$ mm, 24.0–96.0 mm, $n = 12$) (Almasan and Vasiliu, 1967). With the sagittal crest length of 98.8 mm, Bukovynka individual slightly exceeds the range of modern females, but simultaneously is shorter than in Mount Ventoux males and very similar in length to other postglacial female skull from Schlüssellochhöhle im Laubensteingebiet near Frasdorf ($L = 97.5$ mm) (von den Driesch and Vagedes, 1994).

We also compared measurements taken from Bukovynka skull with averages calculated for collected sets of other female skulls (Table 3). Considering dimensions obtained for all five distinguished groups, we found that the Bukovynka cranium dated to the postglacial period was similar to other Late Glacial–Postglacial skulls in the more number of measurements (c1–c5 and c18) than to other groups: Late Pleistocene skulls from Spain (c14, c20, m5 and m8) and Late Pleistocene skulls from other European sites (c19). It indicates that the Bukovynka skull fits well its own 'stratigraphic age' group in spite of a considerable size variation of brown bear skulls.

Apart cranial dimensions and morphology, also teeth can be used to sex recognition in brown bear, although the dimorphism is generally weak (the difference in canine and carnassial between sexes is 1.04) (Gittleman and Van Valkenburgh, 1997; Baryshnikov

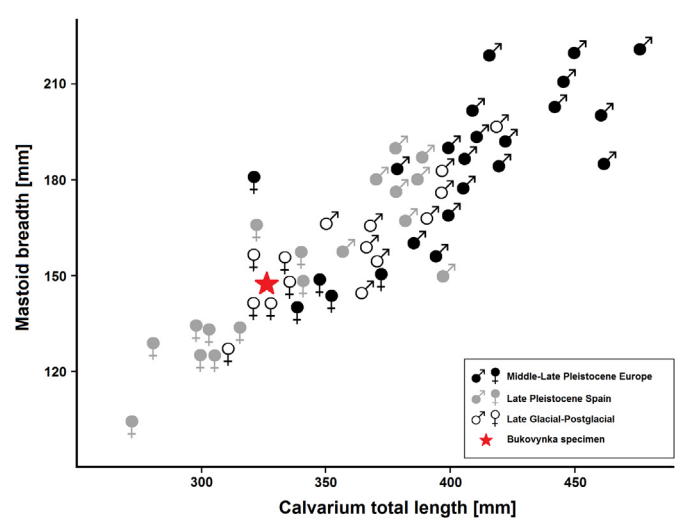

Fig. 6. Total skull length and mastoid breadth scatter plot of the Pleistocene and Holocene European brown bear *Ursus arctos*. For measurements schema see Fig. 3.

et al., 2003). Despite a relatively large size as for a female, canines of Bukovynka individual are long (LC1 = 18.7 mm) but narrow (BC1 = 12.8 mm), which is typical for females rather than males (Crégut et al., 2001; Chaix and Valton, 2007; Villaluenga, 2011). Base on all features described above, we attributed the brown bear skull from Bukovynka Cave to a large, adult brown bear female, prime in the moment of her death.

3.2. Size variability in the course of time based on cranial material

To study variation in skull size we grouped specimens according to their sex, geographic and stratigraphic affiliation. In the case of male skulls we determined seven groups: Middle Pleistocene (MP), Late Middle Pleistocene (LMP), Late Pleistocene from Spain (LPS), Late Pleistocene from other European sites (LP), Late Glacial–Postglacial (LGP), Holocene (H) and Recent (R). Female skulls were clustered into the same groups as males with exception to MP and LMP sets. Summary statistics for these groups is given in Tables 1 and 2 whereas metric features that differentiated significantly the compared groups in Table 3. Box plots for selected metric features were presented in Figs. 7 and 8.

More statistically significant differences were observed between the male rather than female skull groups. The Middle Pleistocene male skulls with the mean total length 454.1 mm were the largest in almost all dimensions from other groups. Although they were significantly greater from slightly younger LMP skulls only in viscerocranium length (c7 measure) and internal length C1–M2 (m6), they exceeded other groups in more than 10 features, usually in global skull length measures (c1, c2, c3) as well as in rostrum (c10) and palatal length (c11). The Late Middle Pleistocene (mean c1 = 412.8 mm) and Late Pleistocene (mean c1 = 414.8 mm) crania sets did not differ significantly between themselves but were much larger from the LPS, LGP, H and R groups. In the case of the LMP, most probably as result of the small sample, the differences were significant for much less measures (usually c1) than for the LP set, which differed in many skull length measures (c1, c2, c3, c11) as well as maximal breadth of occipital condyles (c13) and mastoid breadth (c14). The LP set is quite diverse because includes both few relatively small skulls (with total length < 400 mm) and several exceptionally large specimens from Gargas (c1 = 450.0 mm) (Baryshnikov, 2007) and Bohdalec (c1 = 452.0 mm) (Kafka, 1901). Interestingly, crania from the Late Pleistocene of Spain were significantly smaller (mean c1 = 373.9 mm) from skulls with the comparable age from other sites in Europe (LP set). None of LPS crania exceeded 400 mm in the total length. In addition to the measures listed above, they showed shorter upper tooth row length (m7) and upper molars row length on alveoles (m8) than the LP group. However, the LPS set usually did not differ from Late Glacial–Postglacial crania (mean c1 = 374.6 mm). Only, its basicranial length (c4) was significantly greater. In turn, the LGP group was mostly larger than the Holocene skulls (mean c1 = 358.3 mm) for different measures but only for frontal breadth (c20) the difference was significant because of very small number of specimens in the latter set. The smallest dimensions were observed for recent skulls which significantly differed by many metric features from other groups with exception to Holocene crania, which were significantly larger from the recent set only in mastoid breadth (c14). Interestingly, the recent skulls had one dimension, i.e. maximal breadth at the canine alveoli (m3) significantly wider than those from Late Pleistocene of Spain.

Among studied female skulls, the largest were those from Late Pleistocene of Europe (mean c1 = 348.5 mm). They differed significantly in global skull length (c1, c2 and c3) and maximal breadth of occipital condyles (c13) from crania with the similar age found in Spain (LPS) with mean total length 310 mm. The LP skulls were also greater in many dimensions than crania dated to Late Glacial–Postglacial (mean c1 = 327.6 mm), however, the differences were not statistically significant, probably as a result of small sample number. Averages of many features measured from the LPS skulls were smaller than the LGP crania but the differences were not significant too. In contrast to that, significant differences were found for basicranial (c4) and rostrum dimensions (c10), which were longer in the LPS than LGP group. In turn, the LPG crania were greater than Holocene skulls (mean c1 = 308.1 mm) in all twelve measures although no difference was significant. The smallest dimensions were found for recent skulls, (mean c1 = 295.7 mm) which created a significantly separated set from others in many measures. However, it should be noted that the recent crania showed on average the longest external length C1–M2 of all other sets and had significantly larger maximal breadth at the canine alveoli than the LPS crania.

Considering comparisons of measurements from male skulls of brown bear, we can order them in the following ranking: MP > LMP ≈ LP > LPS ≥ LGP > H ≥ R. It means that Middle Pleistocene crania are significantly larger than others. Late Middle Pleistocene and European Late Pleistocene skulls are comparable in size but are much greater than Late Pleistocene skulls found in Spain. Other groups can be arranged in the following order based on the slightly decreasing skull measurements: Late Glacial–Postglacial, Holocene and recent. A similar order for female skulls is: LP > LPS ≥ LGP > H ≥ R. The metric features that best support the decreasing trend in skull size in time are shown in Figs. 7 and 8.

However, some measures did not follow this trend and did not differentiate brown bear skulls based on their size. These measures were: breadth of foramen magnum (c15), postorbital least breadth (c19) and length of P4 (PM). The lack of changes in these measurements may be explained by 'evolutionary mosaicism'. Not all cranial features are strictly correlated with each other and must be subjected to the same evolutionary trends. The measures that did not follow the evolutionary trend are not strictly related with typical cranial features. The breadth of foramen magnum is rather related with the diameter of medulla oblongata and the postorbital least breadth with the size of brain. The substantial decrease of these features would influence these components of nervous system, which probably was not favored. The other measure that did not differentiate brown bears either is the length of P4, a typical dental feature. It indicates that the teeth size, as a result of dietary requirements, remained rather stable in the time of brown bear evolution in contrast to the skull.

Similar statistical analyses considering the Late Pleistocene group as the whole set showed very similar results (Table 3). Although generally small skulls from Spain were mixed with the larger ones from other European sites, the differences between the Late Pleistocene group and others still remained.

In Fig. 9 we presented clustering of all studied skull groups based on averages of different measures. Two main significant clusters can be recognized. One includes larger and older males skulls dated to Middle, Late Middle and Late Pleistocene (with exclusion of Spain sites). Other, smaller and younger skulls are grouped in the second main cluster with recent male skulls branching off from its base. Skulls with general medium size create a subclade, which includes male skulls from the Late Glacial–Postglacial, the Late Pleistocene of Spain and Holocene as well as female skulls from the Late Pleistocene and Late Glacial–Postglacial. Another separate subclade includes the smallest on average crania from the Late Pleistocene of Spain, Holocene and contemporary female bears.

To further study the general trends in brown bear size during the time, we calculated Spearman correlation coefficient for

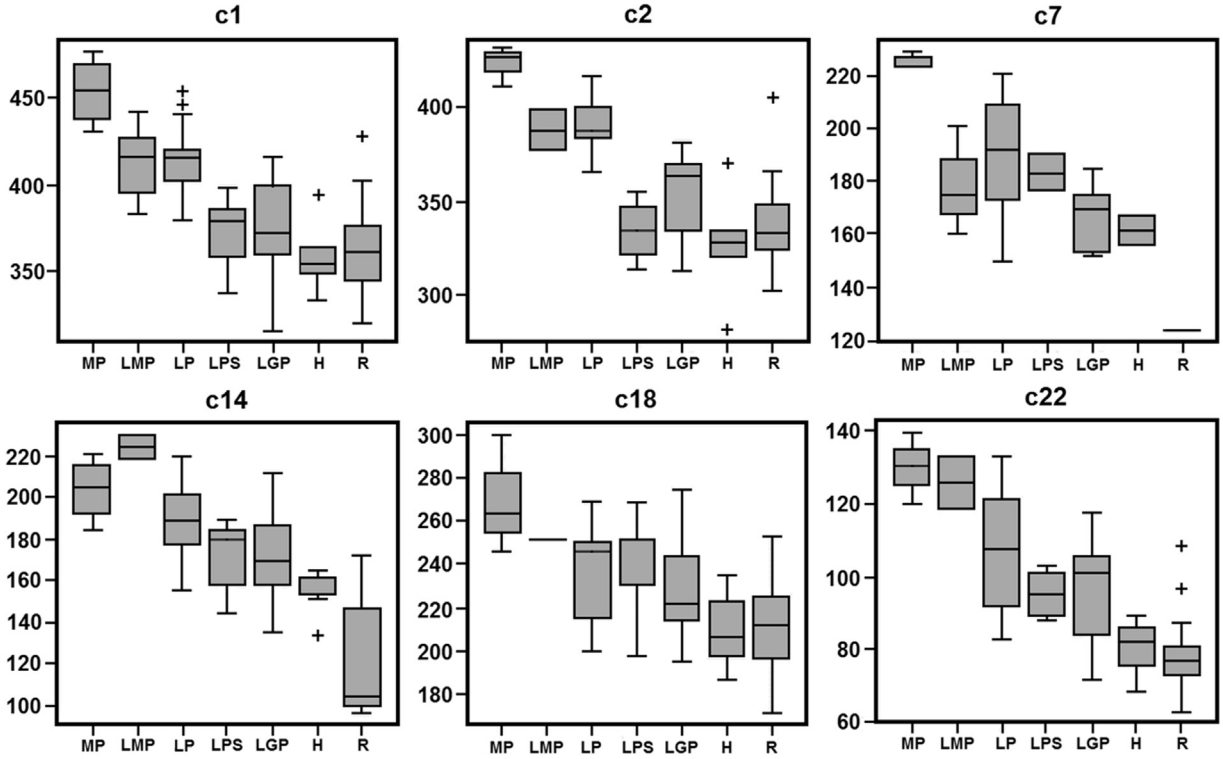

Fig. 7. Box-plots of selected cranial measurements for male skulls divided in groups according to geographic location and stratigraphic position: Middle Pleistocene (MP), Late Middle Pleistocene (LMP), Late Pleistocene (LP), Late Pleistocene in Spain (LPS), Late Glacial Postglacial (LGP), Holocene (H) and Recent (R). For measurements schema see Fig. 3. The thick line indicates median, the grey box shows quartile range and the whiskers determines the range without outliers.

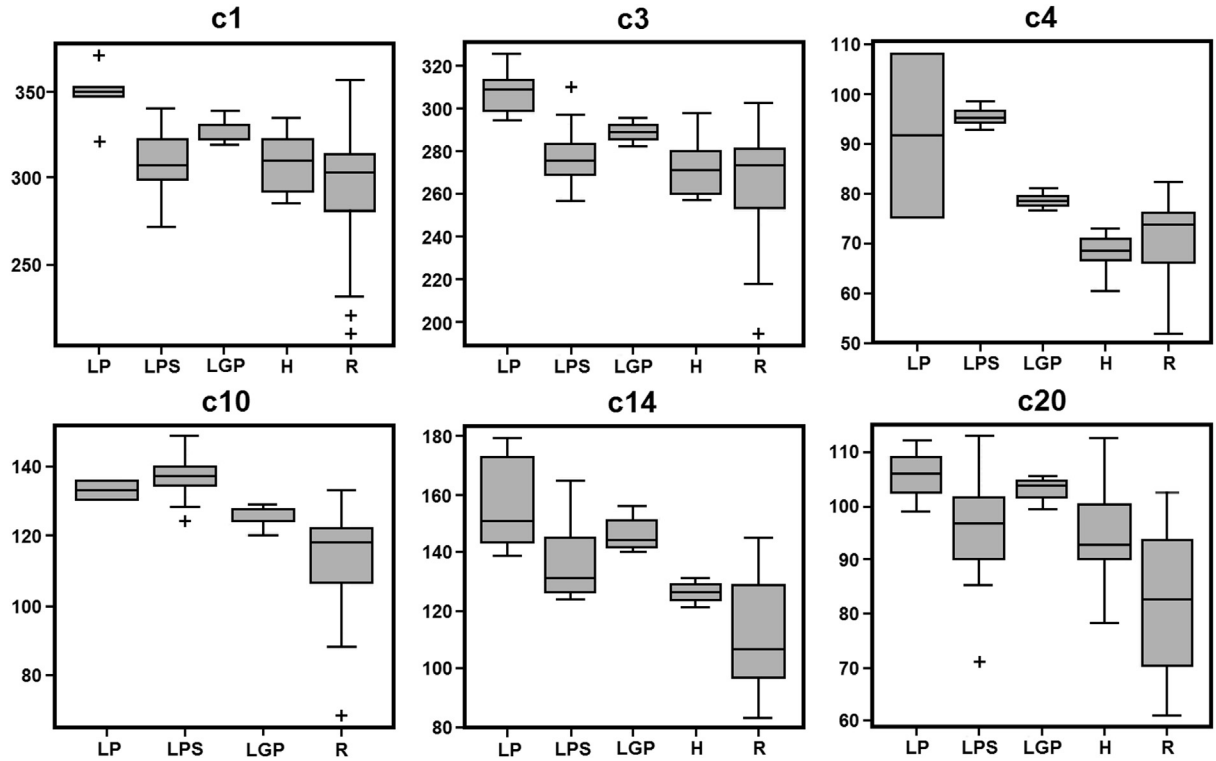

Fig. 8. Box-plots of selected cranial measurements for female skulls divided in groups according to geographic location and stratigraphic position: Late Pleistocene (LP), Late Pleistocene in Spain (LPS), Late Glacial Postglacial (LGP), Holocene (H) and Recent (R). For measurements schema see Fig. 3. The thick line indicates median, the grey box shows quartile range and the whiskers determines the range without outliers.

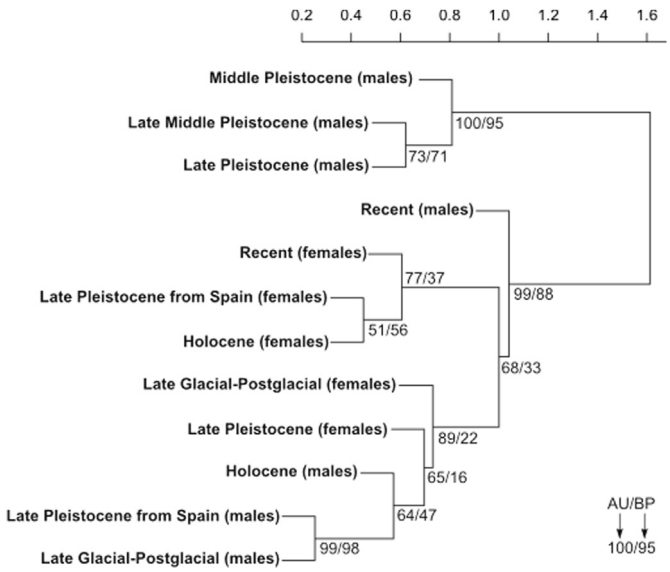

Fig. 9. UPGMA dendrogram clustering brown bear skulls divided into several groups according to their sex, geographic locality and stratigraphic position. Numbers at nodes correspond to *p*-values expressed as percentages calculated using approximately unbiased test (AU) and bootstrap resampling (BP), respectively.

particular measurements, which were ranked based on chronological affiliation of their skulls (Table 3). Almost every correlation coefficient showed a negative value, which indicates a general decreasing trend in the size of brown bear skull during evolution. Most of these coefficients were statistically significant. A significant positive correlation revealed only maximal breadth at the canine alveoli (m3) both in males and females as well as external length C1–M2 (m5) in females. These two measures correspond to dental rather than typical cranial features and could be related with some modifications in dietary habits resulting from climatic changes.

4. Discussion

It is not clear when the oldest *U. arctos* forms from arctoid lineage appeared in Europe. The undoubtedly true brown bears are attributed to the late Middle Pleistocene i.e. layers 19 a–b at Biśnik Cave (Marciszak et al., 2011), Pinilla de Valle (Alférez et al., 1985) and Hunas (Hilpert, 2002). Nevertheless, according to Rabeder et al. (2009), brown bear or at least forms very close to *U. arctos* were already present in Europe at the end of the Early Pleistocene. The same was also pointed out by Pacher (2007). This view is in agreement with divergence time, 1.2–1.7 million years ago, between speleolid and arctoid lineage based on palaeontological (Kurtén, 1968a,b, 1977; Rabeder et al., 2009) and molecular data (Loreille et al., 2001; Bon et al., 2008), although some calculations showed an earlier split about 2.8 million years ago (Krause et al., 2008).

Till now three chrononosubspecies/chronoforms are recognized in the European *U. arctos* lineage since the early Middle Pleistocene. The earliest form, known as *U. arctos kamiensis* (*Ursus kamiensis* sensu Vereshchagin, 1959) was a real giant, characterized by quite considerable sloping of the frontal skull profile and robust build (Vereshchagin, 1959; Baryshnikov and Boeskorov, 2004). To the second subspecies, formerly ascribed to *U. arctos priscus* Goldfuss, 1818, are usually assigned late Middle and especially Late Pleistocene European bears. These forms are also characterized by large size (but in general smaller than *U. arctos kamiensis*) and quite primitive morphology (e.g. the presence of additional upper and lower premolars). Finally, postglacial and Holocene (subfossil) brown bear is described as a nominative subspecies *U. arctos arctos* Linnaeus, 1758 (Sabol, 2001a, 2001b). It differs from the closely related *U. arctos priscus* by somewhat smaller size, smaller number (or even lack) of additional upper premolars (P1–P3) and the more moderate constriction of the skull (Sabol, 2001a, 2001b). Fossil European brown bears were described by many authors under different names (e.g. *Ursus ferox*, *taubachensis*, *horribilis* etc.) (see Erdbrink, 1953 and reference therein; Pacher, 2007). Erdbrink (1953: 321) noted: "No other bear has been the cause of so much nomenclatorial confusion and general controversy". The taxonomical nature of the Pleistocene bears was widely discussed by e.g. Erdbrink (1953) and Pacher (2007), and in general point of view authors agree with Baryshnikov and Boeskorov (2004) and Baryshnikov (2007) in recognition of three different fossil brown bear forms.

Detailed metrical and morphological analysis showed, that *U. arctos kamiensis* differs significantly from European Pleistocene brown bears, but morphologically resembles modern subspecies called Kamchatka bear (*U. arctos beringianus*) (Baryshnikov and Boeskorov, 2004). Both subspecies are similar in palatal proportions, great size and first of all quite convex frontal skull profile (Baryshnikov and Boeskorov, 2004). However, the authors noted, that limited number of the examined samples, cannot give very reliable conclusions. Findings of European brown bear skulls, dated to Middle Pleistocene, are also very rare. Till now only five, more or less complete individuals are known. All those skulls are characterized by great size (total skulls length between 384.0 and 442.0 mm) and are represented by adult males. Although close in dimensions, these individuals differ significantly in the shape of frontal calvarium profile. While European specimens from Hunas, Biśnik Cave and Pinilla del Valle have elongated and quite shallow frontal profile, both Russian individuals (from Ulakhan-Orto-Stan River and Karmalki) are characterized by much more convex part of the cranium when compared to other brown bears. Their overlapping geographical range and possible connection to Eastern bears (close to *U. arctos kamiensis* and modern *U. arctos beringianus*) are responsible for these intermediate features. This hypothesis need of course more numerous samples and for now is still an open question. A curious case represents a bear specimen that has neither stratigraphical position nor label about its geographical locality. It is usually enigmatically called "*Ursus arctoideus*" because is somewhat similar to cave bears (e.g., in size) but shows more features of brown than cave bears. This individual was classified by Kempe et al. (2005) as cave bear (possible female), but four major morphological features indicates rather a large male of the Late Pleistocene brown bear. Its skull shows the narrow and long rostrum, great dimensions with the total calvarium length more than 400.0 mm, the presence of all additional upper premolars (P1–P3) as well as the elongated and relatively flat forehead in the lateral view.

Findings of Late Pleistocene brown bear skulls are more numerous than those from Middle Pleistocene, but still are rare. The Late Pleistocene brown bears are represented for example by specimens classified to subspecies *U. arctos priscus* from Zoolithen Cave (Goldfuss, 1823; Pacher, 2007), Maspino (Koby, 1944), Grotte de Malarnaud (Couturier, 1948), Vyvieranie Cave and Važec Cave (Sabol, 2001a), Murygino (Baryshnikov and Boeskorov, 2004) and Winden (Thenius, 1956). To *U. arctos priscus* should probably be also assigned specimens described as "*U. arctoideus*". We do not re-open a discussion on taxonomical position of these Late Pleistocene brown bears and agree with Pacher (2007 and references therein) about superior position of this name for these fossil bears. However, she also pointed that (Pacher, 2007: 337): " a revision of *U. priscus* and its synonyms is needed".

Records of fossil brown bears from West Europe are much more numerous that those from Central or East Europe. However, only

few of them have more or less certain stratigraphical position, such as specimen from Grotte de L'Herm (Filhol, 1878) or Grotte de Chauvex (Philippe and Fosse, 2003). Stratigraphical age of other individuals, especially those from Ireland and Great Britain, seems to be more uncertain. Although most authors confirmed "Pleistocene" (Late Pleistocene *sensu lato*) age of these bears, the stage of preservation and some accompanying species showed, that some of them can be regarded as postglacial. Apart from the huge bear from Gargas (450.0 mm) no of these specimens exceed 400.0 mm in the total skull length; the largest individuals varied between 380.0 and 395.0 mm. Similar small forms of brown bears were found in Iberian Peninsula. Recently this area has been inhabited by very small subspecies, with average male body mass of ca. 100 kg (Jakubiec, 1993). Although the Late Pleistocene specimens, from Spanish locality Sima de Illobi (Villaluenga, 2011) or some individuals described by Torres Pérez Hidalgo (1988a, 1988b, 1988c, 1988d, 1988e, 1988f) show significantly larger dimensions than Holocene and modern brown bears from Iberian Peninsula, they are still smaller than specimens with the comparable stratigraphic age from other regions of Europe, as it is indicated by our studies. Similarly to British Isles, the Iberian Peninsula, separated from the rest part of Europe by Pyrenean Mountains, has slightly different ecological environmental conditions than more north- and eastern European areas. Late Pleistocene brown bears from Spain also do not exceed 400.0 mm in the total length of male calvarium.

Degerbøl (1933) described seven calvarii of brown bear from Danish sites, and among them two with great dimensions. Both specimens match in size great Late Pleistocene bears. Stratigraphical age of these large individuals was briefly mentioned as postglacial or latest part of Late Glacial, after Last Glacial Maximum (Degerbøl, 1933). Degerbøl (1933) assigned these bears as a new subspecies *U. arctos nemoralis*, characterized by great size and particularly large teeth dimensions, but Baryshnikov (2007) reclassified them as a synonym of *U. arctos priscus*. The presence of these big brown bears in postglacial period of Denmark should be regard as a relict survival.

Large size was regarded as one of the typical features distinguishing Late Pleistocene brown bears from the older ones (e.g. Adams, 1880; Gaudry, 1887; Reynolds, 1906; Freudenberg, 1914; Degerbøl, 1933; Koby, 1944; Erdbrink, 1953; Thenius, 1956; Kurtén, 1959; Sabol, 2001a; Baryshnikov and Boeskorov, 2004; Pacher, 2007; Turner, 2009). Kurtén (1968a, 1968b, 1977, 1978) pointed out the great size of the Late Pleistocene bears and, suggested that the largest individuals were typical of cold periods. Most of the authors cited above also suggested the decreasing body size of brown bear in the transition from last glacial to postglacial period.

Based on analyzes of *U. arctos* skull dimensions, Kurtén (1959, 1968a) proposed a scenario of decreasing body size in the course of brown bear evolution. In order to verify this hypothesis, we compared numerous, homogeneous and sexed samples of brown bear skull dimensions classified according to geographic and stratigraphic affiliation. The studies showed the clear general decreasing trend in size from the Middle Pleistocene through the Late Pleistocene and postglacial to the Holocene skulls both in male and female skulls. Significant deviation represented specimens from excavation sites in Spain dated to the Late Pleistocene, which were smaller from skulls of the comparable age from other European sites or even slightly younger from the Late Glacial and postglacial period for some metric features. These trends were observed both for male as well as female skulls for the most of metric characteristics. A lack of statistically significant difference for some comparisons resulted likely from too small number of available brown bear specimens.

Molecular analyses of Pleistocene and Holocene brown bears demonstrated the fluent gene flow between bear populations in all Europe. Brown bear is highly mobile species (Jakubiec, 1993; Baryshnikov, 2007) and it is not surprise that, for example, a specimen found in the Basque Country shared a Russian haplotype (Valdiosera et al., 2007; Valdosera et al.,, 2008; Edwards et al., 2013). The first mitochondrial DNA analysis of recent European *U. arctos* recognized two main groups, a western (subclade 1a and 1b) and an eastern group (subclade 3a) (Kohn et al., 1995). However, new studies (Valdiosera et al., 2007; Bray, 2010; Davison et al., 2011) showed, that the idea of separate refugees of brown bears during the LGM (Hewitt, 2000) is not so clear (Döppes and Pacher, 2013). Analyses of material from two Austrian sites, Ramesch-Knochen Cave and Windener Bären Cave, also showed the existence of two different lineages at ca. 40,000 BP (Hofreiter et al., 2004). All these studies indicated that *U. arctos* evolved through the Late Pleistocene probably without sufficient barriers to gene flow and the different brown bear lineages in continental Europe likely do not represent evolutionary significant units. Therefore, the observed decreasing size process should be considered a general trend and response for the climatic instability during the Pleistocene rather than some relationships with genetic affiliations. The only exception can represent brown bears from Iberian Peninsula which significantly decreased their size in comparison to populations inhabited the rest territory of Europe in the Late Pleistocene. Such global trend was not observed in the case of cave bear. However, Baca et al. (2012) found some significant differences in molar measures between genetically distinct lineages of cave bear, not only high-alpine forms with reduced body size, *Ursus spelaeus eremus* and *U. s. ladinicus*, but also two main haplotype groups *Ursus ingressus* and *U. spelaeus*.

5. Conclusions

Cosmopolitan, Holarctic *U. arctos* is characterized by extraordinary geographical and individual variability. Analysis of large crania series taking into consideration sexual dimorphism, geographic locality and stratigraphic position showed that brown bear was comparatively large throughout the Pleistocene and its size significantly dropped through the postglacial to the Holocene. The trend concerned both males and females of brown bear, and was associated with climatic changes during the period. An exception from this rule showed skulls found in Spain and dated to the Late Pleistocene, which were significantly smaller than their time equivalents in other European regions. The deviation resulted probably from restricted gene flow between the Iberian and other European populations. To verify the presented views, more abundant cranial material from different localities with precise stratigraphic position and dating are necessary. The same concerns to the taxonomical position of different ancient brown bear forms, especially of *U. arctos priscus* Goldfuss, 1818.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2014.09.052.

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