



TAXONOMIC REVISION OF BEARS FROM THE LOCALITY ŠANDALJA I (CROATIA) AND ITS BIOSTRATIGRAPHIC CONSEQUENCES

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Abstract: Šandalja I palaeocave (“fossil” cave), situated in the southern part of the Istrian peninsula (Croatia), is a well-known locality due to the abundant fossil remains extracted from the bone breccia. It is broadly accepted that the fauna is Middle Villafranchian in age. Since the beginning, the taxonomic status of bear remains has caused controversy and, as a consequence, different authors listed between one to three bear species from this site. Detailed revision of dental material confirmed the presence of two bear species – *Ursus thibetanus* and *U. deningeri*. On the other hand, the previously reported presence of *U. etruscus* was refuted. Subsequently, based on the presence of these two bear taxa, the age of the whole faunal assemblage was re-evaluated and determined as Middle Pleistocene (Toringian).

Key words: *Ursus thibetanus mediterraneus*, *Ursus deningeri*, Middle Pleistocene, Toringian, Šandalja I, Croatia, biostratigraphy

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Introduction

The precise stratigraphic determination of faunal assemblages is of great importance for the correct interpretation of migration events and evolution of particular taxa/lineages during the European Pleistocene. As a consequence, and especially in the case of animals of greater interest, e.g., *Ursus* or *Homo*, the stratigraphic determination of a number of localities has been the subject of long-term controversies. For these localities, different ages were suggested by different authors, often with only limited evidence to support their opinions. With respect to these localities, where possible, the best way to corroborate the previously published dates is to carry out a new detailed taxonomic re-evaluation of the available fossil record.

One of such localities is Pleistocene Šandalja I palaeocave or “fossil” cave in western Croatia. This locality, situated about 4 km southeast from the town of Pula (southern Istrian peninsula), was discovered in 1961 during quarry mining on the eastern slope of St. Daniel hill (Crnolatac and Malez 1961, Malez 1975). The interesting fauna, originating from bone breccias, was excavated and studied by Malez (1975, 1986

etc.; see also Brajković 1998 for review), who suggested an Early/Middle Villafranchian age for this fauna. Among other items, a human tooth and tool were also reported from this locality (Malez 1975). Although the assigning of the tooth to the genus *Homo* was dismissed (Wolpoff 1996: 485), the presence of a tool is generally accepted (e.g., Valoch 1995, Galanidou 2004, etc.).

Still more interesting and surprising is the supposed co-existence of three bear species at this locality – *U. thibetanus* CUVIER, 1823, *U. etruscus* CUVIER, 1823 and *U. deningeri* VON REICHENAU, 1904 (Malez 1975). Especially the co-existence of the two last mentioned species is unexpected, as *U. deningeri* is considered to be a descendent of *U. etruscus* by many authors (Kurtén 1976, Argant 1991, Torres 1992, Baryshnikov 2007, Rabeder et al. 2010). Moreover, the Villafranchian age proposed by Malez (1975) is in accordance only with the presence of *U. etruscus*. Spassov (2000), in view of this fact, suggested that the bear remains probably belong to only one polymorphic bear population of a younger age (ca. 1.2–1.0 Ma). On the other hand, Wagner et al. (2012) presented preliminary results supporting the presence of two bear species (see below) and a Middle

Pleistocene age for this locality.

In the present paper we describe and discuss in detail the available ursid craniodental material from Šandalja I locality and refine the previous taxonomic and stratigraphic results.

Material and methods

The studied material is stored at the Institute for Quaternary Palaeontology and Geology of the Croatian Academy of Sciences and Arts (Zagreb, Croatia). As the studied specimens do not have specific inventory numbers, we identified them using the capital letters A–H. In addition to the material described in this paper, a milk canine and a few postcranial bones are also present in the collection. Moreover, Malez (1975: 186) listed the following specimens, which were not available during our revision in 2007: fragment of left maxilla with P4 and M1, I2 sin., I2 dex. and c inf. sin. (isolated upper incisor and lower canine figured by Malez (1975: pl. IV)).

For comparison, we used the following material (1) *U. thibetanus*, both fossil and recent, housed in Zoological Institute RAS (Saint Petersburg, Russia), Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science (Beijing, China), Natural History Museum, University of Florence (Florence, Italy) and Staatliches Museum für Naturkunde Stuttgart (Stuttgart, Germany), (2) *U. etruscus* housed in the Natural History Museum, University of Florence (Florence, Italy) and (3) *U. deningeri* housed in the National Museum (Prague, the Czech Republic).

Capital and lower case letters, I/i (incisors), C/c (canines), P/p (premolars) and M/m (molars), refer to upper and lower permanent teeth, respectively. The terminology and abbreviations for tooth morphology follow Rabeder (1983, 1989, 1999). Teeth measurements are defined according to Rode (1935). See Wagner and Čermák (2012) for additional details.

The definition and subdivision of the Mammal Ages (i.e., Biharian and Toringian) follow Fejfar and Heinrich (1983, 1990) and Fejfar et al. (1998).

Abbreviations

Collections

IGF	Natural History Museum, University of Florence, Florence
NM	National Museum, Prague
SMNS	Staatliches Museum für Naturkunde Stuttgart, Stuttgart
ZIN	Zoological Institute RAS, Saint Petersburg

Dental cusps

EHyd	enthypoconid
EMEd	entmetaconid
End 1/2	entoconid 1/2
EPrd	entprotoconid
Hyd	hypoconid
Med	metaconid
Prd	protoconid

Systematic palaeontology

Order Carnivora BOWDICH, 1821

Family Ursidae FISCHER [DE WALDHEIM], 1814

Subfamily Ursinae FISCHER [DE WALDHEIM], 1814

Genus *Ursus* LINNAEUS, 1758

Ursus thibetanus CUVIER, 1823

Ursus thibetanus mediterraneus MAJOR, 1873

Text-figs 1, 2, 3a, b, f, 4a, 5b, c

- 1967 *Ursus etruscus* CUVIER; Malez, pp. 57, 76. (partim)
- 1968a *Ursus etruscus*; Malez, p. 152. (partim)
- 1968b *Ursus etruscus*; Malez, pp. 205, 208. (partim)
- 1969a *Ursus etruscus*; Malez, pp. 74, 78. (partim)
- 1969b *Ursus etruscus*; Malez, p. B 21/1. (partim)
- 1970 *Ursus etruscus*; Malez, pp. 206, 213. (partim)
- 1970 *Ursus etruscus*; Marković-Marjanović, p. 156. (partim)
- 1971 *Ursus etruscus*; Malez, p. 66. (partim)
- 1974 *Ursus etruscus*; Malez, p. 79. (partim)
- 1974 *Ursus etruscus*; Malez and Malez-Bačić, p. 6. (partim)
- 1975 *Ursus etruscus* CUV.; Malez, pp. 183, 186, 188, 189, 197, 198, pl. IV. (partim)
- Ursus (Euarctos) mediterraneus* MAJOR; Malez, pp. 186, 188, 189, 198.
- Macaca florentina* COCCHI; Malez, pl. II. (partim)
- 1979a *Ursus etruscus*; Malez, pp. 122, 143. (partim)
- 1979b *Ursus etruscus*; Malez, p. 57. (partim)
- Ursus thibetanus mediterraneus*; Malez, p. 57.
- 1979c *Ursus etruscus*; Malez, p. 210. (partim)
- Ursus mediterraneus*; Malez, p. 120.
- 1986 *Ursus etruscus*; Malez, p. 102. (partim)
- Ursus thibetanus mediterraneus*; Malez, p. 102.
- 1996 *Ursus thibetanus*; Crégut-Bonnoure, p. 99.
- 1996 *Ursus etruscus*; Bosinski, p. 55. (partim)
- Ursus (euarctos) mediterraneus*; Bosinski, p. 55.
- 1998 *Ursus etruscus*; Brajković, p. 8. (partim)
- 2000 *Ursus etruscus*; Sáinz de los Terreros, p. 40. (partim)
- 2000 *Ursus* [of similar stage of evolution as bears from Vallonnet and Pirro]; Spassov, p. 108. (partim)
- 2002 *Ursus* [of similar stage of evolution as bears from Vallonnet and Pirro]; Spassov, p. 234. (partim)
- 2003 *Ursus* [of similar stage of evolution as bears from Vallonnet and Pirro]; Spassov, p. 214. (partim)
- 2011 *Ursus* sp.; Kahlke et al., p. 1376. (partim)
- 2012 *U. t. mediterraneus*; Wagner et al., pp. 50, 51
- 2015 transitional stage in *Ursus etruscus*-*U. deningeri* lineage; Vislobokova and Agadjanian, p. 655. (partim)
- 2016a *U. etruscus*-*U. deningeri*; Vislobokova and Agadjanian, p. 195. (partim)
- U. minimus-thibetanus* lineage; Vislobokova and Agadjanian, p. 195.
- 2016b *U. etruscus*; Vislobokova and Agadjanian, p. 196. (partim)
- U. mediterraneus* (= *U. ex gr. minimus*); Vislobokova and Agadjanian, p. 196. (partim)

Material. Isolated m2 dex. (specimen A; Text-fig. 1a), fragment of right hemimandible with worn m2 and m3 and distal root of m1 (specimen B; Text-figs 1b–c, 2a), distal fragment of m1 dex. (specimen C; Text-fig. 1d),

Table 1. Measurements of bear teeth from the locality Šandalja I (Croatia). *U. d.* – *U. deningeri*, *U. t.* – *U. thibetanus mediterraneus*. Measurements in mm.

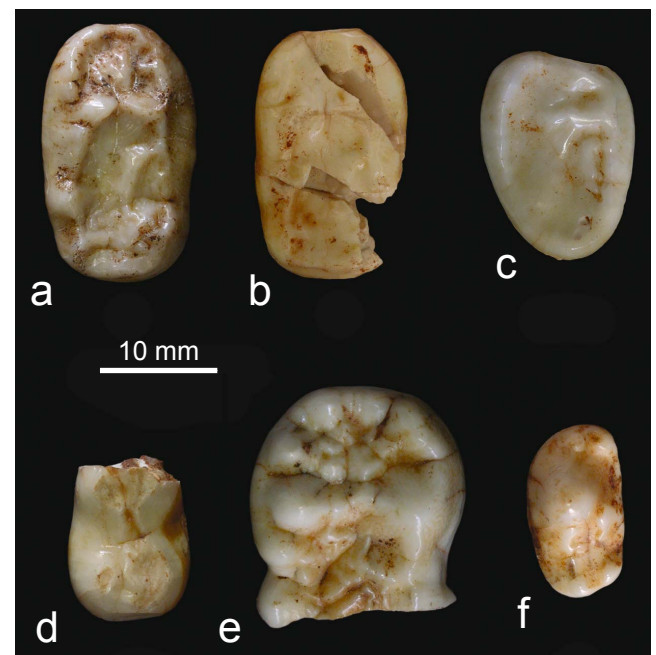
Tooth	Specimen	Species	Maximal length	Buccal length of trigonid	Ligual length of trigonid	Buccal length of talonid	Ligual length of talonid	Maximal width	Trigonid width	Talonid width	Width of constriction	Distance Prd-Med
p4 sin.	H	<i>U. d.</i>	15.0					8.3				
m1 dex.	C	<i>U. t.</i>				6.9				10.8		
m2 dex.	A	<i>U. t.</i>	22.3	15.3	13.5	7.0	8.9	13.6	13.4	12.2	12.4	
m2 dex.	B	<i>U. t.</i>	20.8		10.6		10.2		13.2			
m2. dex.	G	<i>U. d.</i>			16.5				18.5			8.8
m3 dex.	B	<i>U. t.</i>	16.5	9.9		6.6		12.8	12.7			

mesial fragment of right hemimandible with alveoli of p1 – p3 and mesial root of p4 (specimen D; Text-fig. 2b), rostral fragment of mandible with right canine, i3 dex., i2 sin. and alveoli of i1 dex., i2 dex. and i1 sin. (specimen E; Text-fig. 2d) and mesial fragment of left hemimandible with canine and alveoli of p1 – p3 and mesial root of p4 (specimen F; Text-fig. 2c). Specimens B – F possibly belong to the one individual. See Table 1 for tooth measurements.

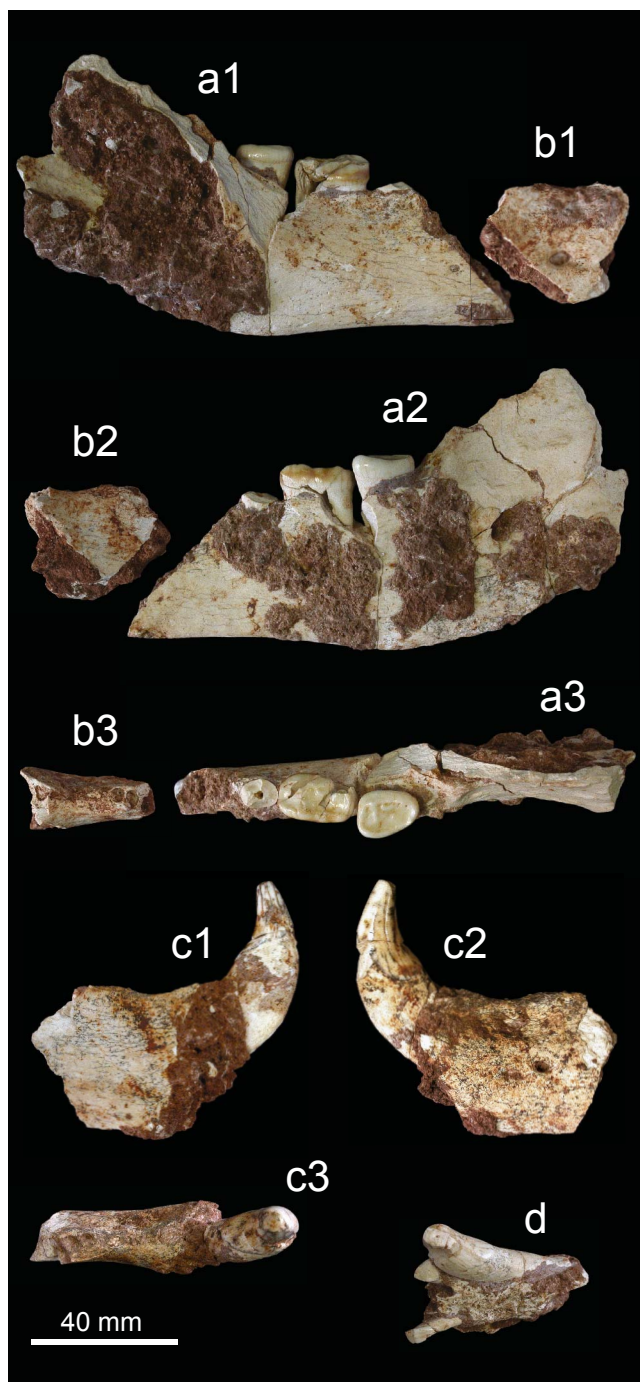
Description. The best preserved specimen is an isolated m2 dex. (specimen A), which is only moderately worn. It has an irregular oval outline, the crown is rather closed with the outer walls diverging laterally (especially the buccal one). There is no cingulum, but the outer walls are wrinkled (the buccal wall more than the lingual). The trigonid is broader than the talonid. The hypoconid area is shortened (distally compressed) compared to the part between Prd-Med and Hyd-End 1 which is relatively elongated. All the main cusps are well developed, but worn. EPrd and EMed (or their precursors) are not orientated perpendicularly to the tooth axis but are directed slightly anteriorly. Elongated swellings/crests project from the medial ends of EPrd and EMed (from the latter a smaller one) and infill most of the anterior trigonid basin. EMed is fully separated from Med, the contact between EPrd and Prd is not visible due to damage. The anterior margin of the tooth is differentiated by small wrinkles. The part of the trigonid distal to Prd-Med is simply built, the dominant structure is well developed mesolophid. The hypoconid is large, rather distally located, a well developed EHd, fully separated from Hyd, is present. End 1 is shorter than End 2. Between End 1 and 2 is a small secondary cusp. With a maximal length 22.3 mm, this tooth is one of the largest found in Europe to date (e.g., Heller 1949, Thenius 1958, Fistani and Crégut-Bonnoure 1993, Crégut-Bonnoure 1996, Turner 2000, Baryshnikov 2007). In its general form as well as in the character of the fine enamel structures, this tooth is very similar to m2 from Grotta di Reale (Italy), the type locality of *U. t. mediterraneus* (Text-fig. 3a, c), but the latter is smaller.

The right mandibular fragment (specimen B) is composed of a horizontal body broken in front of the distal

root of m1 and a part of the vertical ramus (most of the ramus is missing). Processus subalveolaris is present and well developed. m2 and m3 are present. A separated distal fragment of m1 (specimen C) fits well on the preserved m1 distal root fragment. The height of the mandibular body (lingually measured) is, approximately, 38.7 mm under m1/2, 41.2 mm under m2 and 45.4 mm under m3. Malez (1975: 186) reported these specimens as a right mandible with m1 – m3, but on the photo presented (Malez 1975: pl. IV) only m3 and a mesial fragment of m2 are present.



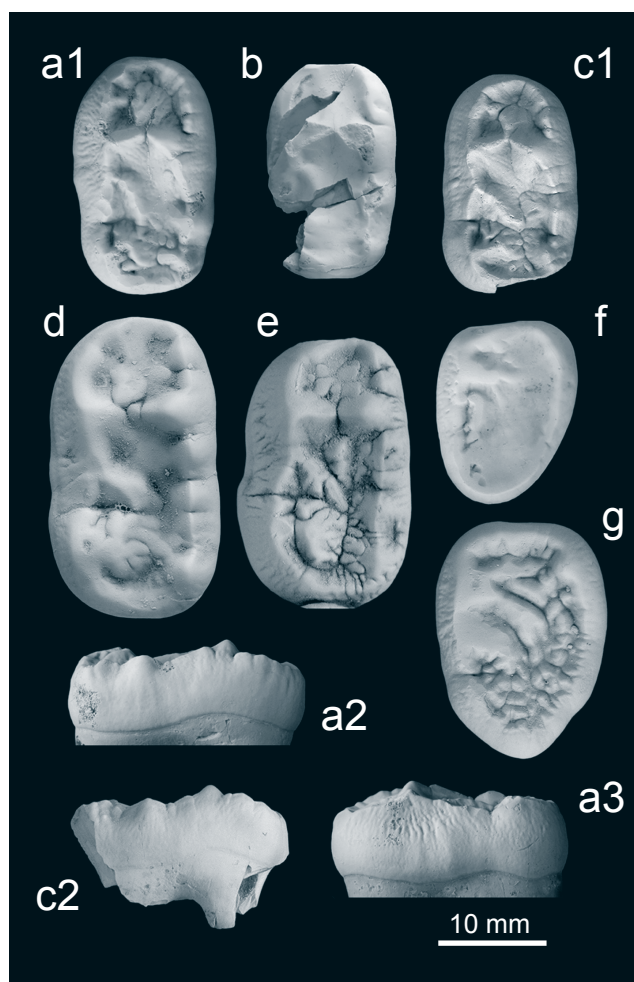
Text-fig. 1. Dental material of ursids from the locality Šandalja I (Croatia) in occlusal view. *U. t. mediterraneus* – a: m2 dex. (specimen A), b: m2 dex., c: m3 dex. (both specimen B), d: distal fragment of m1 dex. (specimen C); *U. deningeri* – e: mesial fragment of m2 dex. (specimen G), f: p4 sin. (specimen H).



Text-fig. 2. Mandibular material of ursids from the locality Šandalja I (Croatia). All specimens represent *U. t. mediterraneus*. a: fragment of right hemimandible (specimen B; 1 – lingual, 2 – buccal, 3 – dorsal view), b: mesial fragment of right hemimandible (specimen D; 1 – lingual, 2 – buccal, 3 – dorsal view), c: mesial fragment of left hemimandible with canine (specimen F; 1 – lingual, 2 – buccal, 3 – dorsal view), d: rostral fragment of mandible (specimen E; dorsal view).

Although all the teeth are heavily worn, they partly bear diagnostic characters (Text-figs 3, 4). Especially important is the distal fragment of m1 with the typical *thibetanus* arrangement (Text-fig. 4). There is a well developed enamel crest connecting Med and Hyd, End 1 is rather small, placed on the linguo-distal corner of the tooth and without any preentoconid structures. The combination of these characters

is diagnostic for *U. thibetanus*. The talonid of this tooth is rather wide (see Tab. 1), in fact wider than in any other studied *U. thibetanus* (except the type of “*U. karabach*” from Azykh Cave, Nagorno Karabakh; Text-fig. 4c; see also Baryshnikov 2010) but as short (buccal length of talonid is 6.9 mm) as in other European specimens of *U. thibetanus* and shorter than in the studied specimens of *U. etruscus* (Olivola, Upper Valdarno). m2 is damaged (the talonid lateral wall and part of enamel on the occlusal surface is missing). It is shorter than specimen A and more rectangular in its shape. Almost no fine enamel structures are apparent due to the strong abrasion (and attrition). m3 is completely preserved but also heavily worn. Its shape is between triangular and egg-like, the buccal wall is wrinkled. Both teeth fit well in their general form with the situation in *U. thibetanus* and differ in the smaller size and simple structure (if it is possible to conclude such information from worn crowns) from *U. etruscus* (Text-fig. 3).



Text-fig. 3. m2 and m3 of *U. t. mediterraneus* from Šandalja I compared with other bear species. a–e: m2, f–g: m3. a: Šandalja I (specimen A; 1 – occlusal, 2 – lingual, 3 – buccal view), b: Šandalja I (specimen B; occlusal view), c: *U. t. mediterraneus*, Grotta di Reale (IGF 4807V; 1 – occlusal, 2 – lingual view), d: *U. etruscus*, Olivola (IGF 4605; occlusal view), e: *U. etruscus*, Upper Valdarno (IGF 908; occlusal view), f: Šandalja I (specimen B; occlusal view), g: *U. etruscus*, Olivola (IGF 4588; occlusal view). Specimens coated by ammonium chloride; a, b, e, f, g reversed.

The right mesial fragment of mandible (specimen D) shows alveoli of all three anterior premolars and of the mesial root of p4, the alveolar margins are generally damaged. The arrangement of premolar alveoli is slightly atypical. There is long diastema between p1 and p2 (10.4 mm), a short one between p2 and p3 (2.4 mm) and p3 is just in front of p4 (distance ca. 0.9 mm). Although a more regular distribution of anterior premolars is usual in Asiatic black bears, a similar situation can also be found, e.g., in one specimen from Mauer (Germany) (Text-fig. 5). A large foramen mentale (ca. 5.8 × 4.1 mm) is located under the alveolus of p2 (Text-fig. 2b2).

A rostral fragment (specimen E) bears c inf. dex., i3 dex. and i2 sin. The crowns of all teeth are heavily worn, the upper part of the canine crown is broken off. The incisor area is laterally compressed and subsequently the alveoli of both p2 sin. and dex. are apparently located distally. The lingual enamel crest is present on the posterior wall in the preserved part of the canine crown. Malez (1975: 184, pl. II) assigned this specimen to *Macaca florentina*.

The last specimen (specimen F), which we assigned to *U. thibetanus*, is the anterior part of a left hemimandible with canine and alveoli of p1 – p3 and mesial alveolus of p4. The alveoli arrangement is the same as in the right fragment (Text-fig. 5). The distance between p1 and p2 is 10.6 mm, between p2 and p3 is 3.5 mm and between p3 and p4 only

1.2 mm. This also supports the idea that specimens B–F belongs to one individual. This specimen is also listed and figured by Malez (1975: 186, pl. IV).

Discussion. The bear specimens described in the previous section were originally (Malez 1975) assigned to two species – *U. thibetanus* (= *Ursus (Euarctos) mediterraneus* in Malez 1975 and others) and *U. etruscus*.

Malez (1975: 186) determined as Asiatic black bear only m2 dex. (specimen A). Despite its relatively large size, its general character (especially oval outline) is rather plesiomorphic. A similar character can also be seen in several Pliocene specimens, but in more evolved species (as well as in many teeth of *U. thibetanus* or Pliocene bears) m2 has a more rectangular shape, with more perpendicular outer (lateral) walls. On the other hand, the fine enamel structure (e.g., well developed mesolophid and secondary structures in the anterior trigonid basin) clearly proves that this specimen is above the evolutionary level of the Pliocene taxa and corresponds to *U. thibetanus*.

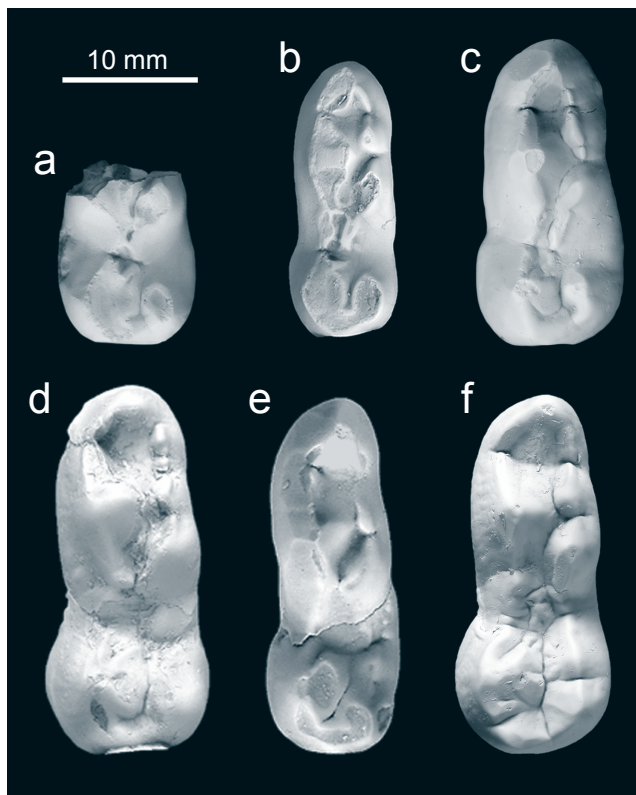
The remaining specimens probably belong to one individual. Although the specimens are rather fragmentary and teeth worn, a taxonomical determination is possible, especially based on the distal fragment of m1. As mentioned above, the combination of (1) End 1 located on the linguo-distal corner, (2) absence of pre-entoconid structures and especially (3) well developed enamel crest connecting the distal end of Med and the basis of Hyd-complex is diagnostic for *U. thibetanus*. Although each of these characters can also be found separately in *U. etruscus* (but some of them at a very low frequency), we have not seen any tooth of this species combining all of them. It is also worth mentioning that none of these fragments/teeth bear any character, which would be known in *U. etruscus* but not in *U. thibetanus*.

Ursus deningeri VON REICHENAU, 1904

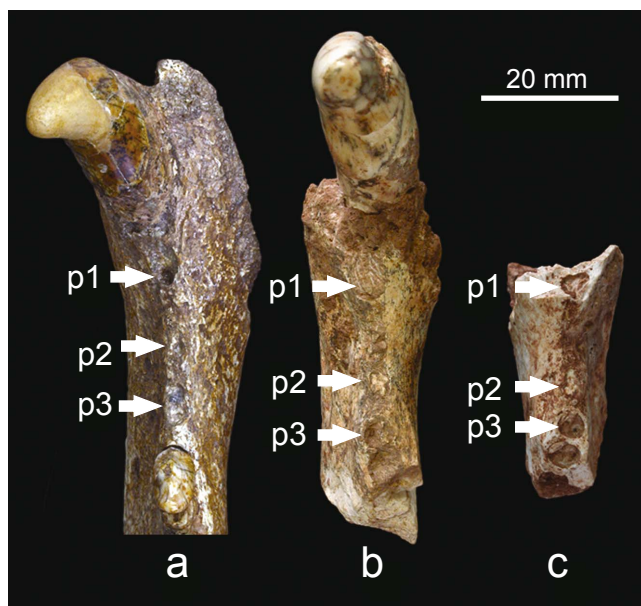
Text-figs 1e, f, 6a, 7a

- 1975 *Ursus* cf. *deningeri* REICHENAU; Malez, pp. 186, 188, 189, 198.
- 1996 *Ursus* cf. *deningeri*; Bosinski, p. 55.
- 2000 *Ursus* [of similar stage of evolution as bears from Vallonnet and Pirro]; Spassov, p. 108. (partim)
- 2002 *Ursus* [of similar stage of evolution as bears from Vallonnet and Pirro]; Spassov, p. 234. (partim)
- 2003 *Ursus* [of similar stage of evolution as bears from Vallonnet and Pirro]; Spassov, p. 214. (partim)
- 2011 *Ursus* sp.; Kahlke et al., p. 1376. (partim)
- 2012 *U. cf. deningeri*; Wagner et al., pp. 50, 51.
- 2015 transitional stage in *Ursus etruscus-U. deningeri* lineage; Vislobokova and Agadjanian, p. 655. (partim)
- 2016a *U. etruscus-U. deningeri*; Vislobokova and Agadjanian, p. 195. (partim)
- 2016b *U. cf. deningeri*; Vislobokova and Agadjanian, p. 196.

Note. As p4 sin. assigned here to *U. deningeri*, was originally determined by Malez (1975) as *U. etruscus*, all the references of *U. etruscus* should be repeated also in synonymy of this species; but we see it as somewhat redundant and we refer here to the synonymy of *U. t. mediterraneus* in this case.



Text-fig. 4. m1 of *U. t. mediterraneus* from Šandalja I compared with other bear species. All teeth in occlusal view. a: Šandalja I (specimen C), b: *U. t. mediterraneus*, Mauer (SMNS 10166), c: *U. t. mediterraneus*, Azykh (ZIN 32549), d: *U. etruscus*, Olivola (IGF 4605), e: *U. etruscus*, Upper Valdarno (IGF 913), f: *U. deningeri*, Koněprusy caves (NM-Rv 20008). Specimens coated by ammonium chloride; a, d, f reversed.



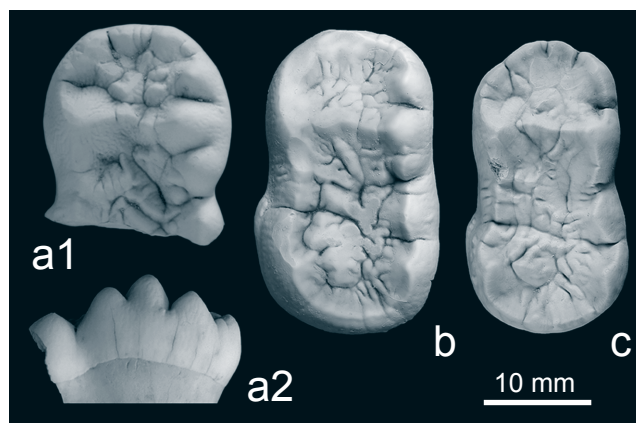
Text-fig. 5. Mesial parts of mandibles of *U. t. mediterraneus* from Mauer (a: SMNS 10166) and Šandalja I (b: specimen F, c: specimen D) showing the arrangement of anterior premolars (p1 – p3). All specimens in dorsal view.

Material. Mesial fragment of m2 dex. (specimen G; Text-fig. 1e) and p4 sin. (specimen H; Text-fig. 1f).

Description. The mesial fragment of m2 dex. (specimen G) is distally limited by breakage extending from the distal part of Prd-complex (in front of contact with Hyd) to the distal arm of End 2. The tooth is only slightly worn. There is a very well developed central constriction. The cusps are well developed and strong. EPrd and EMed are rather low, but clearly separated from Prd and Med. There are well developed secondary cusps and swellings in the anterior trigonid basin and well developed and diversified swellings and crests are also present in the distal part of the trigonid.

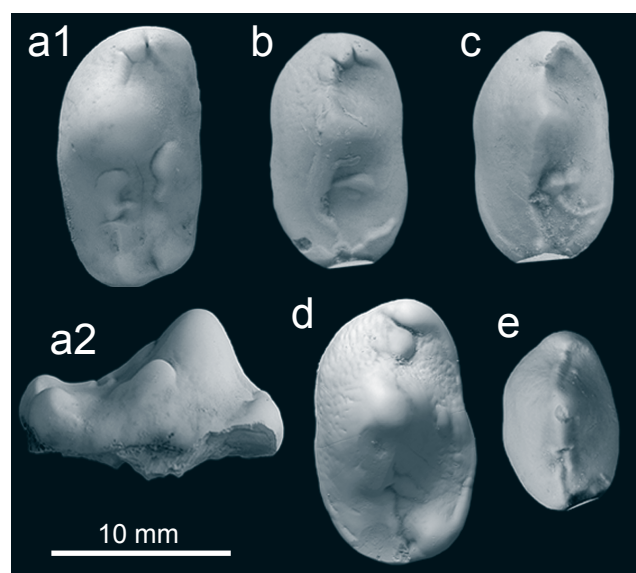
p4 sin. (specimen H) is almost complete (only the lingual crown base is damaged) and only slightly worn. Except the dominant Prd, Pad, Med, Hyd and End are well developed. With the exception of these main cusps, a smaller secondary cusp is developed between Pad and the mesial arm of Prd. The distal arm of Prd is segmented by 2 transverse grooves.

Discussion. The mesial fragment of m2 was already determined as *Ursus* cf. *deningeri* by Malez (1975). Although fragmentary, this tooth has the characters typical for spelaeoid bears, e.g., well developed central constriction, EPrd and EMed forming independent cusps or a highly diversified inner field in the tooth (i.e., not only the presence of crests in the distal part of the trigonid, but also their further divisions, partly forming by small cusps). The combination of these characters is typical for spelaeoid bears and is more advanced compared to *U. etruscus* or even *U. arctos* (cf. Wagner and Čermák 2012). The state of diversification of the inner field seems to be greater than in *U. deningeri* from the beginning of the Middle Pleistocene, i.e., from the Late Biharian (Text-fig. 6). Although we assigned this tooth to *U. deningeri*, it ought to be noted that similar morphology can also be found in some specimens of *Ursus* gr. *spelaeus*. The



Text-fig. 6. m2 of *U. deningeri* from Šandalja I (a: specimen G; 1 – occlusal, 2 – lingual view) compared with Late Biharian *U. deningeri* from C 718 cave (b: NM-R 9740, c: NM-Ra 129; both occlusal view). Specimens coated by ammonium chloride; a reversed.

p4 sin. was assigned by Malez (1975: 186) to *U. etruscus*, but the tooth is more evolved than in this species (Text-fig. 7), where the cusps, other than Prd (and sometimes Pad), are only weakly developed, if not missing. A similar situation is in *U. thibetanus*, in which this tooth is usually even less developed. Even in the type specimen of *U. "karabach"* (= *U. t. mediterraneus*; see Baryshnikov 2010) from Azykh (= Azokh) cave (Nagorno-Karabakh), which has larger and more robust lower teeth than is usual in Asiatic black bear, the p4 is much simpler (although Prd, Hyd and End are present, all of them are only very slightly developed; see Text-fig. 7e). In *U. arctos* this tooth has a not so diversified occlusal surface (at least in most cases). Moreover, relatively



Text-fig. 7. p4 of *U. deningeri* from Šandalja I compared with other bear species. a: Šandalja I (specimen H; 1 – occlusal, 2 – lingual view), b: *U. etruscus*, Casa Frata (private collection), c: *U. etruscus*, Olivola (IGF 4605), d: *U. deningeri*, C 718 cave (NM-Rv 20003), e: *U. t. mediterraneus*, Azykh cave (ZIN 32549) (all in occlusal view). Specimens coated by ammonium chloride; d reversed.

mesially located Med is typical character for spelaeoid bears, distinguishing them from brown bears. On the other hand, compared to the Late Pleistocene *U. gr. spelaeus*, this tooth is rather simple in construction (Pad and Med are smaller). We therefore assigned it to *U. deningeri*.

Discussion

Stratigraphic position of the Šandalja I locality

Originally, the age of Šandalja I locality was supposed to be Middle to Late Villafranchian (Malez 1975, 1986) or Late Villafranchian (Malez et al. 1992). This determination was based on the species composition in this faunal assemblage, consisting mostly of large mammals. Only general information was presented for most taxa, even in the most detailed paper by Malez (1975). In addition to large mammals (e.g. *Canis etruscus*, *Pliocrocota perrieri*, *Chasmaporthetes lunensis*, *Sus strozzi*, etc.; see Mauch Lenardić et al. in press), also *Allocricetus bursae* SCHAUB, 1930 and *Mimomys* sp. are listed. The presence of the latter taxon was based on a mandible with incisor but without molars. Malez (1975: 186) stated that, based on the preserved alveoli, it is apparent that the teeth had roots, but no other information confirming the generic determination are available. Nevertheless, this age was later accepted by many authors (e.g., Valoch 1995, Vislobokova and Agadjanian 2016a, Janković et al. 2016, Pandolfi and Erten 2017). Paunović (2000) or Spassov (2000) proposed the Biharian age for this faunal assemblage (~1 My).

But as stated by several recent authors (e.g., Vislobokova and Agadjanian 2016a, Janković et al. 2016), an up to date revision of the fauna is lacking and its placement in the Late Villafranchian needs reconfirming. Mauch Lenardić et al. (in press) also propose updated determinations, especially for the small mammal representatives. In fact, the only taxon which has been revised in detail so far is *Equus*. Malez (1975) determined the horse species as *Equus stenonis* COCCHI, 1867. Later the material was revised by Forsten (in Malez et al. 1992: 373) with a somewhat different result “It is not clear whether the Šandalja I horse belongs to the stenoid or caballoid group of *Equus*. ... There are some indications that this horse may be a caballoid, although diagnostic lower cheek teeth are lacking: for instance, in the single upper deciduous tooth both labial styles are grooved and the protocone is relatively long...”. Subsequently, the horse was determined as *Equus* sp. Leaving aside the complicated problem of Pleistocene horse taxonomy (for an up-to-date review see Palombo and Alberdi 2017), we wish to note here that caballoid horses are the dominant form recorded in Europe since the Toringian (since ca. MIS 15).

Ursids are other group that complicates the originally accepted stratigraphic assignment. Even Malez (1975: 186) mentioned that *Ursus deningeri* is typical for later faunas but leaves this contradiction unresolved. Later, Spassov (2000, 2002, 2003, in Kahlke et al. 2011) commented that the co-existence of three bear species (as listed by Malez 1975) is doubtful and suggested that the bears from this locality belong to one polymorphic population. He compared them with bears from Pirro Nord (Italy) and Vallonnet (France) and interpreted them as a possible transitional population

from *etruscus*-like bears to some more advance species. Subsequently, he also assumed a similar age for Šandalja I as for the two above mentioned localities, i.e., 1.2–1.0 My.

As documented by Wagner et al. (2012) the presence of Asiatic black bear (*U. thibetanus*) has been recorded in Europe since the Toringian (ca. MIS 15), all of the assumed Biharian (published) records of this species are either misdetermined or based on the material with no diagnostic characters. Spelaeoid bears are known in Europe since the end of the Early Pleistocene (e.g., Moullé 1992, García and Arsuaga 2001, Baryshnikov 2007, Madurell-Malapeira et al. 2009, etc.), and are well recorded since the beginning of the Middle Pleistocene (Late Biharian and Early Toringian) (e.g., von Reichenau 1906, Bishop 1982, Argant 1991, Torres and Cervera 1995, Wagner and Čermák 2012, etc.). The present specimens, although too scarce for ultimate results, in their morphology clearly correspond with typical *U. deningeri* from the Middle Pleistocene, but seem to be more evolved (especially m2) than the Late Biharian representatives. We therefore supposed (in accordance with the preliminary result in Wagner et al. (2012)) that the age of the Šandalja I locality is most probably the Toringian (Middle Pleistocene), as indicated also by Forsten’s revision of horses. The post-Early Pleistocene age is supported also by the evolutionary level of *U. thibetanus*, which is more evolved than its Early Pleistocene (especially Gelasian and early Calabrian) representatives known from China (Pei 1987, Liu and Qiu 2009; pers. obs.). We therefore supposed that an Early Pleistocene age can be excluded for the Šandalja I site, and that this locality yields a Middle Pleistocene (Toringian) faunal assemblage. Detailed revision of the whole fauna is necessary for a more precise stratigraphic placing within this period.

Presence of the Asiatic black bear in the Pleistocene of the Balkan Peninsula

Ursus thibetanus is one of six extant bear species of the subfamily Ursinae nowadays restricted to Asia. Its distribution was more extensive in the past and also included Europe since the Middle Pleistocene (ca. MIS 15) (Wagner et al. 2012 and references therein). During the Toringian, this species was present in many European localities (for reviews see, e.g., Baryshnikov 1992, 2007, 2010, Rustioni and Mazza 1993, Crégut-Bonnoure 1996, 1997, Turner 2000, etc.). In the present paper, we follow Baryshnikov (2010) who accepts only one valid taxon (*U. t. mediterraneus*) for all European and Caucasian finds of *U. thibetanus* (with the exception of *U. t. permjak* BARYSHNIKOV, 2002 from the Ural Mountains – see Baryshnikov (2002, 2007) for details), but other authors recognize more taxa (e.g., Crégut-Bonnoure 1997).

Based on the present revision, Šandalja I locality can be added to the European localities with an unambiguous record of Asiatic black bear. In addition to this locality, *U. t. mediterraneus* is also recorded from several other sites on the Balkan Peninsula.

The first record of this species from this region is in Thenius (1958), who describes a m2 dex. (Thenius 1958: fig. 1) from the **bone breccia near Vrhovlje** (Slovenia), NE of Trieste (Italy). Unfortunately, we were unable to find

this specimen in any collection, but based on Thenius's description, there is no doubt that this specimen belongs to *U. thibetanus*. Except for the tooth itself, there are no additional proxies for its stratigraphic assignment. Thenius (1958) uses the term "Altpleistozän", but this term had another meaning at that time than it does today, as is also apparent, e.g., from Malez (1986), who includes the Cromerian and subsequent glacial events (nowadays recognized as Middle Pleistocene) in it.

Malez (1965) lists "*Ursus cf. mediterraneus*" from the locality **Crvena Stijena** (= Rote Höhle; Montenegro) for the first time. This taxon is also mentioned in his later papers (Basler et al. 1966, Malez 1968b, 1979b, 1986), but in none of them does he give any additional information about particular specimen(s) or include any figure of it/them. Malez (1965, Basler et al. 1966) lists the black bear from layer XXIV. This layer is interpreted as Weichselian by Malez (1965), but Basler et al. (1966: fig. 2) suggests an Eemian age. Later, Malez (1979b, 1986) includes *U. t. mediterraneus* in a faunal assemblage from layer XXV which he correlates with the Saalian (or Riss in his terminology). In both stratigraphic interpretations, the Asiatic black bear is accompanied by brown bear (Malez 1965, 1979b). The Toringian age of the site, leaving aside a more precise stratigraphic determination for the moment, does not contradict the known temporal distribution of this species in Europe (although the Weichselian record has not been unequivocally proven). While there is no particular information about the specimen(s) on which the record is based and with respect to the co-occurrence with brown bear, we suppose that this locality cannot be accepted as a confirmed record of this species. Only a revision of the specific material could confirm/disprove the presence of *U. thibetanus* at this locality.

The other locality which yielded the Asiatic black bear, is **Petralona cave** (Greece). Kurtén and Poulanos (1977, 1981) assign to this species M1 dex. (No. 151) and a small navicular bone (both specimens were found during the new excavations started in 1968). M1 originated from the breccia layers (layers 2–3) in group B (Poulanos (1996) states layer 2, Section Alfa), the navicular bone is from group D–E (layers 14–20) but without more precise specification (Poulanos (1996) quoted layers 16–20, Section Alfa). Based on the measurements and photo (unfortunately not very informative) presented by Kurtén and Poulanos (1977: 64–65), we agree with their assignment of this M1 to *U. thibetanus*. Kurtén and Poulanos (1977) assume that the age of the respective layers (group B) is Elsterian, which fits well within the known distribution of *U. thibetanus* in Europe. Despite the continuing debate about the exact age of particular layers and finds from Petralona cave (see, e.g., Galanidou 2004, Crégut-Bonnoure and Tsoukala 2005, Poulanos 2005, Harvati 2016 and references therein), there is a consensus that most of the fossiliferous layers and especially their upper part are of Toringian age. A larger number of *U. deningeri* were found together with *U. thibetanus* in group B (Kurtén and Poulanos 1977, 1981). Concerning the navicular bone, except for its small size, Kurtén and Poulanos (1977: 65) give no other diagnostic characters. For this reason, we suppose it will be necessary to make a more detailed comparison and description of

this specimen before it is unambiguously assigned to that species. The age of the lower layers is more problematic. The Middle Pleistocene is very probable, based on both numerical dating (see discussion in Poulanos 2005) and the faunal assemblage (e.g., large number of *U. deningeri*). But it is not clear if these layers belong to the Late Biharian or Early Toringian. In any case, the presence of Asiatic black bear in these layers cannot be considered proven, based on the published data. Poulanos (1996: 156) assumes that several specimens determined by Tsoukala (1989: 57, 1991) as *Ursus cf. arctos* (material from Sickenberg's excavations) also belong to *U. thibetanus*. In fact, there is no reason to doubt the taxonomic determination made by Tsoukala (1989, 1991) and, moreover, a new revision (Baryshnikov and Tsoukala 2010) confirms the presence of *U. arctos* and absence of *U. thibetanus* in Sickenberg's collection.

An important record of Asiatic black bear in the Balkans is recorded from the **Gajtan cave** (or Gajtan I) near Shkoder (Albania). Systematic excavations were made by A. Fistani between 1981–1989 (Fistani 1987, 1993a, 1996), and yielded a rich faunal assemblage, with *Ursus thibetanus* as the most interesting find. Remains of *U. thibetanus* were found in two places within the cave (Fistani 1993a, Fistani and Crégut-Bonnoure 1993): (1) in a smaller lateral cavity (called "poche" in Fistani and Crégut-Bonnoure 1993) and (2) in the sedimentary sequence (layers Dh and Dh1) of the main entrance (called "entrée" in Fistani and Crégut-Bonnoure 1993). In the first location, there were found: (a) a cranium with missing rostral part bearing P4 – M2 dex. and alveoli of P1 – P3 (no. 81/3) (figured also in Fistani 1993b: fig. 17B), (b) left hemimandible with c inf., p4 – m2 and alveoli of p1 – p3 and m3 (no. 81/1) and (c) Mtt III sin. (no. 81/4; as 81/7 in the caption to fig. 19/2 in Fistani and Crégut-Bonnoure 1993). In the second location, there were recorded (d) scapholunatum dex. (no. 83/7) and Mtt III sin. (no. 83/46). Detailed description, comparison and figuring by Fistani and Crégut-Bonnoure (1993) leave no doubt that these specimens belong to *U. thibetanus*. In addition to this bear, *U. cf. deningeri* and *U. arctos* were also recorded from this locality (Fistani 1990, 1993a, b, 1995, Fistani and Crégut-Bonnoure 1993). The age of this locality is assumed to be Middle Pleistocene in general, Holsteinian in particular (Fistani 1993b, Fistani and Crégut-Bonnoure 1993). Fistani (1996) interprets the faunal assemblage as a forest fauna from a warm period.

Recently, a possible occurrence of Asiatic black bear is mentioned from the locality **Mishin Kamik cave** (Bulgaria). The excavations started in 2013 (Ivanova et al. 2014) and later *Ursus cf. thibetanus* was included in the preliminary faunal list for the layers 4–6 (Gurova et al. 2016). Furthermore, spelaeoid bears are present in the same faunal assemblage (Gurova et al. 2017, Spassov et al. 2017). A late Middle Pleistocene age has been assumed for this fauna (Gurova et al. 2017, Spassov et al. 2017).

In addition to the above discussed records, the presence of *thibetanus*-like bears (under different names) was introduced also from several Early Pleistocene localities from the Balkan Peninsula. But, in fact, no Biharian specimens bearing diagnostic characters of *U. thibetanus* were so far published (see Wagner et al. 2012 for details).

Conclusion

The available ursid dental and mandibular material from the locality Šandalja I has been revised and its taxonomical status was re-evaluated. We can confirm the presence of *Ursus thibetanus mediterraneus* and *U. deningeri* at this site. The specimens previously assigned to *U. etruscus* were re-determined and assigned to *U. thibetanus* with the exception of a p4 belonging to *U. deningeri*. Based on the presence of these species and their morphological characteristics, the age of the whole faunal assemblage is estimated to be Toringian (Middle Pleistocene) and not Villafranchian (Early Pleistocene) as traditionally stated in the literature. This result is supported by the proven presence of *U. thibetanus* in the other Balkan localities which are all referred to the Middle Pleistocene.

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References

- Argant, A. (1991): Carnivores quaternaires de Bourgogne. – Documents des Laboratoires de Géologie de Lyon, 115: 1–301.
- Baryshnikov, G. F. (1992): *Ursus mediterraneus* v pleystotsene Kavkaza i zamechanya po istorii melkikh medvedey Evrazii [*Ursus mediterraneus* in the Pleistocene of the Caucasus and comments on the history of small bears of Eurasia]. – Trudy Zoologicheskogo Instituta Rossiyskoy Akademii Nauk, 238(1991): 3–60. (in Russian)
- Baryshnikov, G. (2002): The Pleistocene black bear (*Ursus thibetanus*) from the Urals (Russia). – Lynx, n. s., 32(2001): 33–43.
- Baryshnikov, G. F. (2007): Semeystvo Medvezh'i (Carnivora, Ursidae) [Bears Family (Carnivora, Ursidae)] (Fauna Rossii i sopredel'nykh stran, N. S., no. 147 [Fauna of Russia and Neighbouring Countries, N. S., no. 147]). – Nauka, St. Petersburg, 541 pp. (in Russian)
- Baryshnikov, G. F. (2010): Middle Pleistocene *Ursus thibetanus* (Mammalia, Carnivora) from Kudaro caves in the Caucasus. – Trudy Zoologicheskogo Instituta Rossiyskoy Akademii Nauk, 314: 67–79.
- Baryshnikov, G. F., Tsoukala, E. (2010): New analysis of the Pleistocene carnivores from Petralona Cave (Macedonia, Greece) based on the Collection of the Thessaloniki Aristotle University. – Geobios, 43: 389–402. <https://doi.org/10.1016/j.geobios.2010.01.003>
- Basler, D., Malez, M., Brunnacjer, K. (1966): Die Rote Höhle (Crvena Stijena) bei Bileća/Jugoslawien. – Eiszeitalter und Gegenwart, 17: 61–68.
- Bishop, M. J. (1982): The Mammal Fauna of the Early Middle Pleistocene Cavern Infill Site of Westbury-Sub-Mendip, Somerset. – Special Papers in Palaeontology, 28: 1–108.
- Bosinski, G. (1996): Les origines de l'homme en Europe et en Asie. – Editions Errance, Paris, 176 pp.
- Brajković, D. (1998): Šandalja. – Histria Archaeologica, 29: 5–25. (in Croatian)
- Crégut-Bonnoure, E. (1996): A review of small Middle Pleistocene bears from France. – Acta zoologica cracoviensia, 39(1): 89–101.
- Crégut-Bonnoure, E. (1997): The Saalian *Ursus thibetanus* from France and Italy. – Geobios, 30(2): 285–294. [https://doi.org/10.1016/S0016-6995\(97\)80234-3](https://doi.org/10.1016/S0016-6995(97)80234-3)
- Crégut-Bonnoure, E., Tsoukala, E. (2005): The Pleistocene Caprinae (Mammalia, Bovidae) from the Petralona Cave (Macedonia, Greece): new interpretation and biogeographical implications. – In: Crégut-Bonnoure, E. (ed.), Les ongulés holarctiques du Pliocène et du Pléistocène, Actes colloque international Avignon, 10–22 septembre 2000. Quaternaire, hors-série 2: 161–178.
- Crnolatac, I., Malez, M. (1961): Ein neuer Fundort pleistozäner Fauna in Südistrien. – Bulletin scientifique, Conseil des académies de la RSF de Yougoslavie, Section A, Sciences naturelles, techniques et médicales, 6(2): 33–34.
- Fejfar, O., Heinrich, W.-D. (1983): Arvicoliden-Sukzession und Biostratigraphie des Oberpliozäns und Quartärs in Europa. – Schriftenreihe für Geologische Wissenschaften, 19/20: 61–109.
- Fejfar, O., Heinrich, W.-D. (1990): Proposed biochronical division of the European continental Neogene and Quaternary based on Muroid rodents (Rodentia, Mammalia). – In: Fejfar, O., Heinrich, W.-D. (eds), International Symposium Evolution, Phylogeny and Biostratigraphy of Arvicoliden (Rodentia, Mammalia). Geological Survey, Prague, pp. 115–124.
- Fejfar, O., Heinrich, W.-D., Lindsay, E. H. (1998): Updating the Neogene rodent biochronology in Europe. – Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO, 60: 533–554.

- Fistani, A. (1987): Gjetje fosilesh me interes paleoetnologjik nga shpella e Gajtanit (Shköder) [Fossil finds of Paleolithic interest from Gajtan cave (Shköder)]. – Buletini shkencor, 24(1): 117–132. (in Albanian)
- Fistani, A. (1990): *Ursus deninger* von Reicheneneau nga shpella e fosileve – Gajtan (Shkodër) [*Ursus deninger* von Reicheneneau from the fossils cave of Gajtan – Shkodra]. – Buletin i shkencave natyrore, Seria B: Kimi – Biologji, 44(4): 53–63. (in Albanian with English abstract)
- Fistani, A. (1993a): Découverte d'un humerus d'ursidé à l'olécrâne perforé dans le site de Gajtan I (Shkodër) en Albanie du nord. – L'Anthropologie, 97(2/3): 223–238.
- Fistani, A. (1993b): Human evolution in Albania for the Quaternary period. – In: Sigmon, B. (ed.), Before the wall fell: The science of man in socialist Europe. Canadian Scholars Press, Toronto, pp. 141–178.
- Fistani, A. (1995): The large mammals of the Middle Pleistocene from Gajtan I cave Shkoder, North Albania: The first Pleistocene mammals from Albania, southeast Europe (Preliminary report). – Kuntari, 7: 3–9.
- Fistani, A. (1996): *Sus scrofa priscus* (Goldfuss, de Serres) (Mammalia, Artiodactyla, Suidae) from the Middle Pleistocene layers of Gajtan 1 site, southeast of Shkodër (north Albania). – Annales de Paléontologie, 82(3): 177–229.
- Fistani, A., Crégut-Bonnou, E. (1993): Découverte d'*Ursus thibetanus* (Mammalia, Carnivora, Ursidae) dans le site pléistocène moyen de Gajtan (Shkoder, Albanie). – Geobios, 26(2): 241–263.
[https://doi.org/10.1016/S0016-6995\(93\)80018-M](https://doi.org/10.1016/S0016-6995(93)80018-M)
- Galanidou, N. (2004): Early Hominids in the Balkans. – In: Griffiths, H. I., Kryštufek, B., Reed, J. M. (eds), Balkan Biodiversity. Pattern and Process in the European Hotspot. Springer, Dordrecht, pp. 147–165.
https://doi.org/10.1007/978-1-4020-2854-0_9
- García, N., Arsuaga, J. L. (2001): *Ursus dolinensis*: a new species of Early Pleistocene ursid from Trinchera Dolina, Atapuerca (Spain). – Comptes Rendus de l'Académie des Sciences, Paris, Sciences de la Terre et des planètes – Earth and Planetary Sciences, 332(2001): 717–725.
[https://doi.org/10.1016/S1251-8050\(01\)01588-9](https://doi.org/10.1016/S1251-8050(01)01588-9)
- Gurova, M., Ivanova, S., Spassov, N., Hristova, L., Krumov, I., Verheyden, S., Marinova, E., Dedov, I. (2016): Prouchvane na peshterata Mishin kamik – sezon 3 [Excavations at Mishin Kamik Cave – 2015 season]. – Archaeological Discoveries & Excavations in 2015: 56–58. (in Bulgarian with English abstract)
- Gurova, M., Ivanova, S., Spassov, N., Hristova, L., Popov, V., Marinova, E., Böhme, M. (2017): Prouchvane na peshterata Mishin kamik – sezon 4 [Excavations at Mishin Kamik Cave – 2016 season]. – Archaeological Discoveries & Excavations in 2016: 48–50. (in Bulgarian)
- Harvati, K. (2016): Paleoanthropology in Greece: Recent Findings and Interpretations. – In: Harvati, L., Roksandic, M. (eds), Paleoanthropology of the Balkans and Anatolia. Human Evolution and its Context. Springer, Dordrecht, pp. 3–14.
https://doi.org/10.1007/978-94-024-0874-4_1
- Heller, F. (1949): *Ursus (Plionarctos) stehlini* Kretzoi, der kleine Bär aus den altdiluvialen Sanden von Mauser-Bammental und Mainz-Wiesbaden. – Sitzungsberichte der Heidelberger Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, Jahrgang 1949 (Abh. 11): 449–508.
- Ivanova, S., Krumov, I., Spassov, N., Hristova, L., Madeonska, J., Gurova, M., Straigt, D. (2014): Archaeologicheski prouchvaniya v peshterata Mishin kamik, Chiprovsko [archaeological excavation at Mishin kamik cave, Chiprotsi area]. – Archaeological Discoveries & Excavations in 2013: 31–33. (in Bulgarian)
- Janković, I., Ahern, J. C. M., Karavanić, I., Smith, F. H. (2016): The Importance of Croatian Pleistocene Hominin Finds in the Study of Human Evolution. – In: Harvati, K., Roksandic, M. (eds), Paleoanthropology of the Balkans and Anatolia. Human Evolution and its Context. Springer, Dordrecht, pp. 35–50.
https://doi.org/10.1007/978-94-024-0874-4_3
- Kahlke, R.-D., García, N., Kostopoulos, D. S., Lacombe, F., Lister, A. M., Mazza, P. P. A., Spassov, N., Titov, V. V. (2011): Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. – Quaternary Science Reviews, 30: 1368–1395.
<https://doi.org/10.1016/j.quascirev.2010.07.020>
- Kurtén, B. (1976): The Cave Bear Story. – Columbia University Press, New York, 163 pp.
- Kurtén, B., Poulanos, A. N. (1977): New stratigraphic and faunal material from Petralona Cave with special reference to the Carnivora. – Anthropos, Athens, 4(1-2): 47–130.
- Kurtén, B., Poulanos, A. N. (1981): Fossil Carnivora of Petralona Cave: Status of 1980. – Anthropos, Athens, 8: 9–56.
- Liu, J., Qiu, Z. (2009): Carnivora. – In: Jin, C., Liu, J. (eds), Paleolithic Site – The Renzidong Cave, Fanchang, Anhui Province. State Key Project of the 9th five year plan – Origin of Early Humans and Environmental Background (Series monograph, no. IV). Science Press, Beijing, pp. 220–283 + 412–423. (in Chinese with English summary).
- Madurell-Malapeira, J., Alba, D. M., Moyà-Solà, S. (2009): Carnivora from the late Early Pleistocene of Cal Guardiola (Terrassa, Vallès-Penedès Basin, Catalonia, Spain). – Journal of Paleontology, 83: 969–974.
<https://doi.org/10.1666/09-054.1>
- Malez, M. (1965): Crvena Stijena in Montenegro – eine bedeutende paläontologische Lokalität aus der Balkanhalbinsel. – Bulletin scientifique, Conseil des académies de la RSF de Yougoslavie, Section A, Sciences naturelles, techniques et médicales, 10(5): 145–147.
- Malez, M. (1967): Donjopleistocenska fauna koštane breče kod sela Dubci u Dalmaciji [Early Pleistocene fauna from bone breccia near Dubci in Dalmatia]. – Rad Jugoslavenske akademije znanosti i umjetnosti, 345: 55–100. (in Croatian with German summary)
- Malez, M. (1968a): Die altpleistozänische Vertebratenfauna in dem Gebiete des Dinarischen Karstes. – Bulletin scientifique, Conseil des académies de la RSF de Yougoslavie, Section A, Sciences naturelles, techniques et médicales, 13(5-6): 152.

- Malez, M. (1968b): O razvoju kvartara na području Vanjskih Dinarida [About the development of Quaternary in the area of Dinaric Alps]. – In: Prvi Kolokvij o geologiji Dinaridov, I. del [First colloquy on Geology of Dinaric Alps, Vol. 1]. Geological Survey and Geological Society of Slovenia, Ljubljana, pp. 203–210. (in Croatian with German summary)
- Malez, M. (1969a): Donjopleistocenske faune vertebrata na području Dinarskog krša [Early Pleistocene vertebrate fauna from the Dinaric Karst]. – In: III. Simpozij Dinarske Asocijacije [3rd Congress of Dinaric Association]. Institut za geološka istraživanja, Zagreb, pp. 73–80. (in Croatian with German summary)
- Malez, M. (1969b): Die altpleistozänen Wirbeltierfaunen aus den Höhlen von Kroatien. – In: 5. Internationaler Kongress für Speläologie (Stuttgart 1969), Abhandlungen, 4. Sektion: Biospeläologie. Mangold in Komm., Blaubeuren, pp. B 21/1–B 21/6.
- Malez, M. (1970): Pećinska nalazišta donjopleistocenskih fauna na području Dinarskog krša [The Early Pleistocene vertebrates localities in caves of Dinaric Karst]. – In: Congrès Yugoslave de spéléologie, cinquième session. Skopje, pp. 205–214. (in Croatian with German summary)
- Malez, M. (1971): Naseljavanje Dinarskog krša u pleistocenu [The colonization of Dinaric Karst in the Pleistocene]. – In: Simpozij o zaštiti prirode u našem kršu (1970) [Symposium about the nature protection in our karst]. Jugoslavenska akademija znanosti i umjetnosti, Odjel za prirodne nauke, Zagreb, pp. 63–80. (in Croatian with English summary)
- Malez, M. (1974): Über die Bedeutung der Entdeckung von Geröllgeräten in den Villafranchiumsschichten der Šandalja I in Istrien (Kroatien, Jugoslawien). – Bulletin scientifique, Conseil des académies de la RSF de Yougoslavie, Section A, Sciences naturelles, techniques et médicales, 19(3-4): 79–80.
- Malez, M. (1975): O značenju otkrića ostataka roda *Homo* u naslagama vilafranka Šandalje I kod Pule [On the significance of the genus *Homo* discovery in the Villafranchian sediments of Šandalja I near Pula]. – Rad Jugoslavenske akademije znanosti i umjetnosti, 371: 181–201. (in Croatian with English summary)
- Malez, M. (1979a): Osnovne crte paleolitika i mezolitika u Hrvatskoj [An outline of Palaeolithic and Mesolithic in Croatia]. – Rad Jugoslavenske akademije znanosti i umjetnosti, 383: 117–153. (in Croatian with German summary)
- Malez, M. (1979b): Kvartarna fauna Jugoslavije [Quaternary fauna of Yugoslavia]. – In: Basler, Đ. (ed.), Praistorija Jugoslavenskih zemelja. I. Paleolitsko i mezolitsko doba [Prehistory of Yugoslavia. I. Palaeolithic and Mesolithic]. Svjetlost, Sarajevo, pp. 55–79. (in Croatian)
- Malez, M. (1979c): Prirodni okviri [Outline of environment]. – In: Basler, Đ. (ed.), Praistorija Jugoslavenskih zemelja. I. Paleolitsko i mezolitsko doba [Prehistory of Yugoslavia. I. Palaeolithic and Mesolithic]. Svjetlost, Sarajevo, pp. 197–219. (in Croatian)
- Malez, M. (1986): Die quartären Vertebraten-Faunen in der SFR Jugoslawien. – Quartärpaläontologie, 6: 101–117.
- Malez, M., Forsten, A., Lenardić, J. (1992): Fossil horses (Mammalia, Equidae) from the bone breccias of Croatia, northern Balcan. – Paläontologische Zeitschrift, 66(3-4): 369–385.
<https://doi.org/10.1007/BF02985824>
- Malez, M., Malez-Bačić, V. (1974): The Upper Pleistocene Ornithofauna of Šandalja I near Pula in Istria. – Bulletin scientifique, Conseil des académies de la RSF de Yougoslavie, Section A, Sciences naturelles, techniques et médicales, 19(1-2): 6–7.
- Marković-Marjanović, J. (1970): Data Concerning the Stratigraphy and the Fauna of the Lower and Middle Pleistocene of Yugoslavia. – Palaeogeography, Palaeoclimatology, Palaeoecology, 8: 153–163.
[https://doi.org/10.1016/0031-0182\(70\)90008-8](https://doi.org/10.1016/0031-0182(70)90008-8)
- Mauch Lenardić, J., Oros Sršen, A., Radović, S. (in press): Quaternary fauna of the Eastern Adriatic (Croatia) with the special review on the Late Pleistocene sites. – Quaternary International.
<https://doi.org/10.1016/j.quaint.2017.11.028>
- Moullé, P.-E. (1992): Les grands mammifères du Pleistocène inférieur de la grotte du Vallonnet (Roquebrune-Cap-Martin, Alpes-Maritimes). Etude paléontologique des Carnivores, Equidé, Suidé et Bovidé; Ph.D. Dissertation. – MS, Museum National d'Histoire naturelle à l'Institut de Paléontologie Humaine, Paris, France, 365 pp. (copy in private library of JW)
- Palombo, M. R., Alberdi, M. T. (2017): Light and shadows in the evolution of South European stenonoid horses. – Fossil Imprint, 73(1-2): 115–140.
<https://doi.org/10.1515/ifi-2017-0006>
- Pandolfi, L., Erten, H. (2017): *Stephanorhinus hundsheimensis* (Mammalia, Rhinocerotidae) from the late early Pleistocene deposits of the Denizli Basin (Anatolia, Turkey). – Geobios, 50: 65–73.
<https://doi.org/10.1016/j.geobios.2016.10.002>
- Paunović, M. (2000): Cadre biostratigraphique du Pléistocène inférieur et moyen en Croatie. – In: Lumley, H. de (ed.), Actes du Colloque International „Les premiers habitants de l'Europe“. Tautavel, Résumés de communications. Muséum National d'Histoire Naturelle, pp. 64–65.
- Pei, W. (1987): Carnivora, Proboscidea and Rodentia from Liucheng *Gigantopithecus* cave and other caves in Guangxi. – Memoirs of Institute of Vertebrate Palaeontology and Palaeoanthropology, Academia Sinica, 18: 1–134.
- Poulianos, N. A. (1996): Pleistocene Mammals of Petralona Cave, Chalkidiki, N. Greece; Doctoral thesis. – MS, Charles University Prague, Faculty of Natural Sciences, Praha, the Czech Republic, 379 pp. (copy in private library of Prof. I. Horáček, Charles University, Prague)
- Poulianos, N. A. (2005): The absolute datings of Petralona cave. – In: Proceedings of the 14th International Congress of Speleology, vol. 1. Hellenic Speleological Society, Athens, pp. 172–177.
- Rabeder, G. (1983): Neues von Höhlenbären. Zur Morphogenetik der Backenzähne. – Die Höhle, 34(2): 67–85.
- Rabeder, G. (1989): Modus und Geschwindigkeit der Höhlenbären-Evolution. – Schriftenreihe des Vereins zur Verbreitung naturwissenschaftlicher Kenntnisse in Wien, 127:105–126.

- Rabeder, G. (1999): Die Evolution des Höhlenbären-Gebisses. – Mitteilung der Kommission für Quartärforschung der Österreichischen Akademie der Wissenschaften, 11: 1–102.
- Rabeder, G., Pacher, M., Withalm, G. (2010): Early Pleistocene bear remains from Deutsch-Altenburg (Lower Austria). – Mitteilungen der Kommission für Quartärforschung der Österreichischen Akademie der Wissenschaften, 17: 1–135.
- Reichenau, W. von (1906): Beiträge zur näheren Kenntnis der Carnivoren aus den Sanden von Mauer und Mosbach. – Abhandlungen der Großherzoglich Hessischen Geologischen Landesanstalt zu Darmstadt, 4(2): 189–313.
- Rode, K. (1935): Untersuchungen über das Gebiß der Bären. – Monographien zur Geologie und Palaeontologie, Ser. 2, H. 7: 1–162.
- Rustioni, M., Mazza, P. (1993): The Tibetan-like bear from Grotta di Reale Porto Azzurro (Isle of Elba, Italy). – *Il Quaternario*, 6(1): 35–38.
- Saínz de los Terreors, J. Y. (2000): Los Orígenes del Poblamiento Paleolítico en Europa: Una visión bioestratigráfica [The Origins of the Palaeolithic Population in Europe: A Biostratigraphic viewpoint]. – *Espacio, Tiempo y Forma, Serie I, Prehistoria y Arqueología*, 13: 33–49. (in Spanish)
- Spassov, N. (2000): Biochronology and zoogeographic affinities of the Villafranchian faunas of Bulgaria and South Europe. – *Historia naturalis bulgarica*, 12: 89–128.
- Spassov, N. (2002): The Late Villafranchian and biochronology of south-east Europe: faunal migrations, environmental changes and possible first appearance of the genus *Homo* on the continent. – *Annales Géologiques des Pays Helléniques*, 1e série, 39(A): 221–243.
- Spassov, N. (2003): The Plio-Pleistocene vertebrate fauna in South-Eastern Europe and the megafaunal migratory waves from the east to Europe. – *Revue de Paléobiologie*, 22(1): 197–229.
- Spassov, N., Hristova, L., Ivanova, S., Georgiev, I. (2017): First Record of the “Small Cave Bear” in Bulgaria and the taxonomic status of bears of the *Ursus savini* ANDREWS – *Ursus rossicus* BORISSIAK group. – *Fossil Imprint*, 73(3-4): 275–291.
- Thenius, E. (1958): Über einen Kleinbären aus dem Pleistozän von Slowenien, nebst Bemerkungen zur Phylogenese der plio-pleistozänen Kleinbären. – *Razprave, Razred za prirodoslovne in medicinske vede*, 4: 631–646.
- Torres, T. (1992): The European descendants of *Ursus etruscus* C. Cuvier (Mammalia, Carnivora, Ursidae). – *Boletín Geológico y Minero*, 103: 12–22.
- Torres, T., Cervera, J. (1995): Multivariate Analysis of the dental morphology of Plio-Pleistocene Ursids, with some observations concerning the phylogenetic position of *Ursus deningeri* Von Reichenau from Cueva Mayor (Sima de los Huesos, Atapuerca). – In: Bermúdez de Castro, J. M., Arsuaga, J. L., Carbonell, E. (eds), *Human Evolution in Europe and the Atapuerca Evidence*. Junta de Castilla y León, Valladolid, pp. 123–135.
- Tsoukala, E. S. (1989): Contribution to the study of the Pleistocene fauna of large mammals (Carnivora, Perissodactyla, Artiodactyla) from Petralona cave, Chalkidiki (N. Greece). – *Scientific Annals, Aristotle University of Thessaloniki, School of Geology*, 1(8): 1–360 + 62 pls. (in Greek)
- Tsoukala, E. (1991): Contribution to the study of the Pleistocene fauna of large mammals (Carnivora, Perissodactyla, Artiodactyla) from Petralona Cave (Chalkidiki, N. Greece). Preliminary report. – *Comptes Rendus de l'Académie des Sciences, Paris, Sér. II*, 312: 331–336.
- Turner, E. (2000): Miesenheim I. Excavations at a Lower Palaeolithic site in the central Rhineland of Germany. – *Monographien, Römisch-Germanisches Zentralmuseum, Forschungsinstitut für Vor- und Frühgeschichte*, 44: I–VIII + 1–150.
- Valoch, K. (1995): The earliest occupation of Europe: Eastern Central and Southeastern Europe. – In: Roebroeks, W., Kolfschoten, T. van (eds), *The earliest occupation of Europe*. *Analecta Praehistorica Leidensia*, 27: 67–84.
- Vislobokova, I. A., Agadjanian, A. K. (2015): New Data on Large Mammals of the Pleistocene Trlica Fauna, Montenegro, the Central Balkans. – *Paleontological Journal*, 49(6): 651–667.
<https://doi.org/10.1134/S0031030115060143>
- Vislobokova, I. A., Agadjanian, A. K. (2016a): On the History of Early–Middle Pleistocene Mammal Faunas of the Central Balkans. – *Paleontological Journal*, 50(2): 187–201.
<https://doi.org/10.1134/S0031030116020106>
- Vislobokova, I. A., Agadjanian, A. K. (2016b): New Data on Age of the Pleistocene Fauna from the Trlica Locality (Montenegro, Central Balkans) and Its Correlation with Other Faunas of Europe. – *Stratigraphy and Geological Correlation*, 24(2): 188–202.
<https://doi.org/10.1134/S0869593816020088>
- Wagner, J., Čermák, S. (2012): Revision of the early Middle Pleistocene bears (Ursidae, Mammalia) of Central Europe, with special respect to possible co-occurrence of spelaeoid and arctoid lineages. – *Bulletin of Geosciences*, 87: 461–496.
<https://doi.org/10.3140/bull.geosci.1354>
- Wagner, J., Čermák, S., Horáček, I. (2012): The presence of *Ursus ex gr. minimus-thibetanus* in the Late Villányian and its position among the Pliocene and Pleistocene black bears in Europe. – *Quaternaire, hors-série* 4: 39–58.
- Wolpoff, H. M. (1996): *Human evolution*. – McGraw-Hill, Inc., New York etc., 921 pp.