Gimranov, Dmitry; Lavrov, Alexander; Prat Vericat, Maria; [et al.]. «Ursus etruscus from the late Early Pleistocene of the Taurida ave (Crimean Peninsula)». Historical Biology, (May 2022). DOI 10.1080/08912963.2022.2067993

Ursus etruscus from the late Early Pleistocene of Taurida Cave (Crimean Peninsula, Russia)

Dmitry Gimranov[*,1], Alexander Lavrov[2], Maria Prat-Vericat[3], Joan Madurell-Malapeira[3], Alexey Lopatin[2]

[1]Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, 8th March Street 202, 620144 Yekaterinburg, Russian Federation, djulfa250@rambler.ru;
[2]Borissiak Paleontological Institute of Russian Academy of Sciences, Profsoyuznaya 123, 117647 Moscow, Russian Federation;
[3]Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, 08195 Cerdanyola del Vallès, Barcelona, Spain.

*Corresponding author.

Abstract

The present work describes the fossil remains of *Ursus etruscus* from the newly discovered Taurida cave at the north Black Sea area, Crimea. The bone bearing layer of Taurida Cave corresponds to the Psekupian complex of mammals of the regional scale of Eastern Europe and to the Late Villafranchian of Western Europe (ca. 1.8 Ma). Here we describe unpublished dentognathic material of ursids unearthed in the last field surveys performed at the cave, further comparing it with coeval chronologic and geographic sites around Europe. Our anatomical and biometrical analysis suggested the inclusion of the studied specimens in the hypodigm of the Early Pleistocene medium-sized species *Ursus etruscus.*

The finds of the *U. etruscus* from the Southern part of Eastern Europe are a link between the western and eastern parts of the paleobiogeographic range of this species. Therefore, the finds of *U. etruscus* from Crimea are important for understanding the morphological diversity and evolution of *U. etruscus* which is the putative ancestor of both cave and brown bears. Furthermore, the study of these finds is also important for understanding of the processes of the forming of the large mammal assemblages in the late Early Pleistocene and its relation with the dispersal of the genus *Homo*.

Key words: *U. etruscus*, *U. arctos*, cave bears, Early Pleistocene, Crimea peninsula, Taurida Cave

Introduction

Ursus etruscus was a European medium to large sized ursid species earliest recorded at the Middle Villafranchian sites such as Saint-Vallier (ca. 2.2 Ma; France; Viret 1954) or La Puebla de Valverde (ca. 2.1 Ma; Spain, Kurtén and Crusafont 1977). The last chronologically well-constrained records of this species come from the sites of Barranco León and Fuente Nueva-3 (ca. 1.4-1.2 Ma; Spain; Medin et al. 2017). The former species was mainly-recorded in Western Europe, however several sparce finds at Southeast and Central Asia and North Africa, Morocco or China are also noteworthy evidencing a wide biogeographical range during the Early Pleistocene (Baryshnikov 2007; Jiangzuo et al. 2018). Throughout this chronologically long record two different morphotypes of *U. etruscus* can be distinguished: an early forms from the Middle Villafranchian (e.g. Saint-Vallier or Kuruksay) and late forms from Olivola, Pietraffita, Upper Valdarno, Venta Micena or Dmanisi (Mazza and Rustioni, 1992; Baryshnikov 2007; Medin et al. 2017, 2019).

At the end of the Early Pleistocene and roughly coeval with the climatic shifts associated with the '*Early-Middle Pleistocene Transition*' the earliest large and stout specimens of speleoid bears (*Ursus deningeri*) were recorded in Europe at sites such as Le Vallonnet (France; 1.2 Ma; Moullé 1992), Vallparadís Section (1.0-0.8 Ma; Spain; Madurell-Malapeira et al. 2010; 2014) or Untermassfeld (1.0 Ma; Germany; Musil 2001).

In turn, the first European record of the brown bear lineage (*U. arctos*), putatively dispersed from Western Asia, has been a hotly debated topic in the last decades (Mazza and Rustioni 1992, 1994; García and Arsuaga 2001; Musil 2001; Baryshnikov 2007; Rabeder et al. 2010; Wagner and Cermak 2012). Several authors consider the latest Early Pleistocene European forms putatively related with the brown bear lineage including the remains of Deutch-Altenburg, Untermassfeld or Gran Dolina TD6 (Rabeder et al. 2010; Wagner and Cermak 2012; See a review in Madurell-Malapeira et al., in press). However the first undisputed brown bear record in western Europe come from the lower layers of the Caune l'Aragó (ca. 0.5 Ma; Moigne et al. 2006)

Finally, the new finds of *U. etruscus* from Taurida Cave analyzed in the present work are chronologically synchronous with the geographically closer finds of Dmanisi (ca. 1.8 Ma; Georgia) and with the time of the early dispersal of the genus *Homo* in Eurasia. Recently Medin et al. (2019) on the analysis of the Dmanisi ursids discuss on the putative competence of these two omnivorous species for the food resources in harsh environments.

Chronological background and the vertebrate assemblage of Taurida Cave

Taurida Cave was discovered in Crimea during 2018, being located 15 km east of Simferopol (45°02´37"N, 34°17´09"E) at the Crimean Peninsula (Fig. 1). Taurida Cave is located on the Inner ridge of the Crimean Mountains in the interfluves of the Beshterek and Fundukla rivers and was formed in the thickness of the Paleogene nummulite limestones (Simferopol Stage).

The preliminary analysis of the unearthed vertebrate remains from Taurida Cave suggested a Late Villafranchian age for the deposit (Gimranov et al. 2020; Lavrov et al. 2020a, 2020b; Lopatin 2019a, 2019b; Lopatin et al. 2019; Zelenkov et al. 2019). Throughout the Late Villafrachian, the cave was connected to the day surface through a wide (2-3 m wide and about 2-3 m high) horizontal southern corridor, which opened on the slope of the left side of the Pra-Fundukla valley (Oksinenko and Lavrov 2021, in press).

The remains of fossil bears were found by the authors in the near-surface layer of soil in a small cave hall called the "Hyenas Den". The bone-bearing layer of the cave is represented by red-brown loams of subaeral genesis. The faunal list include the species: *Pachystruthio dmanisensis*, *Aix* cf. *galericulata*, *Perdix perdix*, *Tetrao* sp., *Tetrax* cf. *kalmani*, *Otis* aff. *tarda*, *Strix aluco*, *Athene* sp., *Accipiter* cf. *gentilis*, Falconidae gen. et sp. indet., Corvus cf. *corax*, *Hypolagus brachygnathus*, *Hystrix* (*Acanthion*) *vinogradovi*, *Hystrix refossa*, *Canis* sp., jackal-like dog *Canis* sp., *Pachycrocuta brevirostris*, *Homotherium crenatidens*, *Megantereon adroveri*, *Lynx issiodorensis*, *Archidiskodon meridionalis*, *Equus* sp., *Elasmotherium* sp., *Stephanorhinus* sp., *Paracamelus gigas*, *Arvernoceros verestchagini*, *Leptobos* sp. and *Bison* (*Eobison*) sp., *Gazellospira torticornis* and *Pontoceros ambiguus*. The co-occurrence of representatives of *Leptobos* sp. and *Bison* sp. makes it possible to determine the age of the deposits from 1.8 to 1.5 Ma (Lopatin 2019a; Vislobokova et al. 2019, 2020). Analysis of the fauna complex of the Taurida Cave indicates its correspondence to the Psekupian complex of mammals of the regional scale of Eastern Europe, which corresponds to the Late Villafranchian, the zone of mammals MNQ18 of the International scale. The revised Quaternary time scale of Gibbard et al. (2010) for chronological references is used in this text.

Concerning the ursids of Taurida cave, previously we described a fragment of the facial part of the Etruscan bear skull (PIN No. 5644/65) from Taurida Cave (Gimranov et al. 2020). The main diagnostic features of the skull of *U. etruscus* (after Mazza and Rustioni 1992) are as follows: elongated facial part, very small upper premolars which separated by large diastemas, the M1 of rectangular shape with a weak parastyle and metastyle, elongated shape of M2. These features and also the morphology of P4 (protocone position) take the opportunity to identify the skull fragment from the Taurida Cave as *U. etruscus*.

Material and methods

The present study is based on the comparative anatomical analysis of the ursid material from Taurida and other Pleistocene samples from Europe. The two mandibles from Taurida Cave are housed in PIN RAS (Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow) and different tooth is housed in IPAE RAS (Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg). The comparative fossil material from Middle-Late Villafranchian and Epivillafranchian from Eurasia are housed at ICP, MAEG, MPRM, IGF (see abbreviation below) and Dmanisi collections of the S. Janashia Museum of Georgia, Georgian National Museum (Tbilisi). These comparative fossil samples also include specimens of *U. etrusucs* and *U. deningeri* from: the Iberian sites of La Puebla de Valverde, Venta Micena, Fuente Nueva 3, Barranco León, Incarcal Complex, Cueva Victoria and Vallparadís Section; the French sites of Saint-Vallier, Ceyssaguet and Vallonnet; the Italian sites of Olivola, Pirro Nord, Pietrafitta, Monte Argentario and Upper Valdarno Basin and the German site of Untermassfeld (Musil 2001).

Dental size differences between the various bear groups were assessed using two-dimensional plots. All statistical analyses were performed using PAST 3.1 (Hammer et al. 2001).

For dental nomenclature we followed Rabeder (1999) and Jiangzuo et al. (2019).

Dental anatomical abbreviations—lower premolars: p1, p2, p3, p4; lower molars: m1, m2, m3. Dental nomenclature abbreviations: Par, paraconid; Met, metaconid; Prt, protoconid; Hyd, hypoconid; Ent, entoconid.

Institutional abbreviations—D: catalogue number of the Dmanisi collections of the S. Janashia Museum of Georgia, Georgian National Museum (Tbilisi); ICP: Institut Català de Paleontologia Miquel Crusafont (Sabadell, Spain); MAEG: Museo Arqueológico y Etnológico (Granada, Spain); MPRM: Musée de Préhistoire Régionale (Menton, France); IGF: Natural History Museum, Geology and Paleontology Section, University of Florence (Italy);

Due to the fact that researchers do not have an unambiguous opinion about the use of the Latin name for small cave bear *Ursus savini* Andrew, 1922 or *U. rossicus* Borissiak, 1930 (Baryshnikov, 2007; Rabeder et al., 2010; Wagner, Cermak, 2012; Baryshnikov, Puzachenko, 2020) we consider these bears under the name *U.* ex. gr. *savini-rossicus*. Based on the methods of paleoDNA analysis, many species of cave bears are currently isolated (Hofreiter et al. 2007; Krause et al. 2008; Knapp et al. 2009; Stiller et al. 2014; Barlow et al. 2016, 2018, 2020; Knapp et al., 2019). By the reason that not all cave bears from the Late Pleistocene have been genetically studied, we suppose it is possible to consider its as belonging to *U.* ex. gr. *spelaeus-kanivetz*.

Systematic paleontology

Order Carnivora Bowdich 1821

Family Ursidae Fischer de Waldheim 1814

Subfamily Ursinae Fischer de Waldheim 1814

Genus *Ursus* Linnaeus 1758

Ursus etruscus (Cuvier 1823)

Figs. 2, 3 and 4

Referred specimens—left partial ramus with m1-m3 (PIN No. 5644/67; Fig. 2, A-C); Incomplete right and left corpora with both c1 and p4-m1 (PIN No. 5644/66; Fig. 2, D-F); right m2 (IPAE No. 727/69; Fig. 2, G-I)

Measurements—Table 1

Description

Corpus— The specimen PIN No. 5644/67 preserve the left corpus. The corpus is high and have medium degree of robusticity. The specimen belongs to the old individual: m1-m3 are quite worn out. The overall size of the corpus is similar to a large extant *U. arctos*. The anterior margin of the masseter fossa is situated at the level of the middle part of m3 on buccal view. The pterygoid process, an attachment surface of the pterygoid muscle, is situated approximately below the foramen mandibulae. There are four mental foramina, located below diastema of p1-p3 and alveolus of p4. The p1 and p2 alveoli are not preserved, the p3 alveolus is partially preserved. The diastema between the canine and p3 is short, it is only 19.8 mm long.

In the specimen PIN No. 5644/66 the incisors are absent in both corpora. Both c1 are also preserved. Alveoli p1, p4, and m1, and the incomplete alveolus m2 are present in right corpus. The left corpus was broken at the level of the anterior part of the m2 alveolus. There are five mental foramens on the right corpus and four in the left one. The corpora are slender, with a long diastema (Fig. 2).

Dentition—p4 is absent in PIN No. 5644/67, but its alveolus is preserved. The m1 has a hypoflexid. The trigonid of m1 is longer than the talonid, but buccolingually narrower. In the paraconid, the buccal cristid was worned out, the lingual cristid is well pronounced. It is clearly seen that the metaconid was small and unicuspid. The postmetacristid (Rmed2 by Jiangzuo et al. 2019) arises towards the center of the hypoconid. There are no additional structures between metaconid and entoconid. The entoconid complex consists of one cusp. The buccal cingulum arises from the posterior part of the trigonid to the posterior part of the talonid. The m2 has a small hypoflexid. The trigonid is mesiodistally longer than the talonid, the length of the talonid is 39.6% of the total length of the tooth. Also m2 trigonid is buccolingually narrower than the talonid. It is clear that m2 has a entoconid complex consists of a two (entoconid 1 and entoconid

2) cusps whose sizes are approximately equal to each other. The m3 is oval shaped, without a hypoflexid. The metaconid is ridge-like and small.

The specimen No. 5644/66 display a relatively large p1 alveoli. The alveoli p2 and p3 are absent. The p4 is oval shaped, has no additional cusps except for a tiny cusp on the distal cristid of protoconid. In addition, there is a mesial rudimentary cusp in the form of a basal thickening of the main cone. The m1 display the apex of the protoconid poorly distinguishable, the buccal margin of the protoconid is strongly worn out, the lingual margin is preserved and has no additional elements. The m1 has a weakly expressed hypoflexid (possibly due to the tooth is strongly worn out). The trigonid of m1 is mesiodistally longer than the talonid, but narrower than it. The anterior root of m1 is much smaller in size at its base than the posterior root. The m2 is missing, only the alveoli are preserved. Finally, the right m2 No. 727/69 (Fig. 2, G-I) is oval in shape, has a slightly pronounced hypoflexid. The talonid is elongated relative to the trigonid and takes up 36.4% of the total length of the tooth.. The trigonid m2 is somewhat buccolingually narrower than the talonid.. The anterior root is slightly less than the posterior root in width of the base. There is a weak, short cingulum on the buccal side at the point of contact between the trigonid and talonid.

Discussion

Morphological comparisons of the Taurida bears with arctoid and speleoid ursids

Taking into account the large biometrical variability in Quaternary ursids as a consequence of intraspecific variability and sexual dimorphism (Medin et al. 2019; Prat-Vericat et al. 2020), we will focus our taxonomical study on the morphology of the Taurida bear comparing it with known Early Pleistocene European assemblages.

The studied specimens display a high and robust corpora (Fig. 2A,D). The pterygoid process, an attachment surface of the pterygoid muscle (*m. pterigoideus medialis pars anterior*), situated approximately below mandibular foramen, are very marked. This structure is typical of arctoid forms according to Garcia and Arsuaga (2001) and Madurell-Malapeira et al. (2010).

Concerning anterior premolars (p1-p3), the studied specimens show alveolus of p1, p2 and p3 (Fig. 2C, E; Fig. 3). In *U. etruscus* early forms (St. Vallier, Kuruksay) all premolars are present and closely attached to each other (Fig. 3), meanwhile in advanced forms (Dmanisi, Pietrafitta) appeared disatematas between p1-p2 and p2-p3. Later, in Epivillafranchian forms of *U. deningeri* (Vallonnet or Cal Guardiola) these anterior premolars are only present sometimes normally lacking always p2 (Fig. 3; J. M.-M. pers. observ.). The Taurida specimens as clearly visible in Fig. 3 display a distribution and presence of anterior premolars similar to Dmanisi or Pietrafitta.

The p4 of PIN No. 5644/66. display an oval shape in occlusal view, with no additional cusps, except for a tiny cusp on the posterior cristid of protoconid. These features of p4 are characteristic of *U. etruscus* (Baryshnikov 2007; Medin et al. 2019) and distinguish it from the bear species of the spelaeoid linege. The p4 of cave bears are characterized by the presence of additional cusps on the posterior protoconid cristid (posprotocristid), with anterior and posterior additional cusps (Baryshnikov 2007; Rabeder 1999; Wagner and Čermák 2012; Prat-Vericat et al. 2020). The Pleistocene *U. arctos* are characterized by p4 with anterior and posterior additional cusps (Gimranov 2018). Extant *U. arctos* is characterized by p4 without additional cusps on the posterior protoconid cristid (morphotype A2, occurrence 23.8%) or with its presence (morphotype A3, occurrence 36.3%). Note that the early evolutionary stage of the Etruscan bear (St. Vallier and Kuruksay localities) is characterized by p4 with anterior and posterior additional cusps (Viret 1954; Sharapov 2014). The late evolutionary stage of the

Etruscan bear (Upper Valdarno and Dmanisi) is characterized by a simpler p4 structure, without additional cusps (Mazza and Rustioni 1992; Medin et al. 2019).

The Taurida m1's display metaconid (unicuspid) and entoconid (unicuspid) in the specimen PIN No. 5644/67; additional cusps and cristids are absent between the metaconid and entoconid. These features of m1 (Fig. 4,A-E) are characteristic of *U. etruscus* (Mazza and Rustioni 1992; Baryshnikov 2007) and distinguish it from brown and spelaeoid bears (Fig. 4F-N). Fossil and extant *U. arctos* are characterized by m1 (Fig. 4, K-N) with a bicuspid or tricuspid metaconid and bicuspid entoconid (Baryshnikov 2007; Wagner and Čermák 2012). The m1 of speleoid bears (Fig. 4, F-J) are characterized by a developed metaconid with additional cusps and also additional cusps between the metaconid and the entoconid. The m1 entoconid in turn, is bicuspid or more complicated (Baryshnikov 2007; Rabeder 1999; Wagner and Čermák 2012; Prat-Vericat et al. 2020). The metaconid complex of m1 consists of a single cusp in *U. etruscus* PIN No. 5644/67 brings it closer to the finds of *U. etruscus* from St. Vallier and Kuruksay, which belong to the early evolutionary stage of the Etruscan bears (Mazza and Rustioni 1992; Baryshnikov 2007).

The m2 of *U. etruscus* PIN No. 5644/67 has bicuspid entoconid of approximately equal size. A similar structure is typical for *U. etruscus*, *U. arctos* and spelaeoid bears (Mazza and Rustioni 1992; Baryshnikov 2007; Rabeder 1999; Wagner and Čermák 2012; Prat-Vericat et al. 2020). The m2 talonid of PIN No. 5644/67 is moderately short (39.6% of the total tooth length). The short talonid is characteristic of the early evolutionary stage of the Etruscan bears (St. Vallier and Kuruksay). The Etruscan bears of the late evolutionary stage (Upper Valdarno, Olivola, Pietrafita or Dmanisi) are characterized by an mesiodistally elongated talonid m2 (Baryshnikov 2007).

The m3 of *U. etruscus* PIN No. 5644/67 is oval shaped in occlusal view, without hypoflexid. The shape of m3 (PIN No. 5644/67) is similar to m3 of *U. arctos* (Baryshnikov 2007; Wagner and Čermák 2012). At the same time, it differs markedly from cave bears, which have a pentagonal occlusal shape (Rabeder 1999; Wagner and Čermák 2012; Prat-Vericat et al. 2020).

According to the former assertions the Taurida ursid specimens are here included in the hypodigm of *U. etruscus* on the basis of: presence of p1, p2 and p3; a short diastema between c1-p4; a p4 with oval shape and without additional cuspulids and a metaconid and entoconid complexes of m1 containing one cusp each and the absence of additional elements (cusps and cristids) between the metaconid and entoconid. A number of other features, such as a robust corpus, a m1 unicuspid metaconid, and a moderately short talonid m2, also indicates the similarity with *U. etruscus* (PIN No. 5644/67) from Crimea with the subspecies *U. e. verescagini* and *U. e. saintvallierensis*, which are the early evolutionary stage of Etruscan bears (Baryshnikov 2007).

5.2. Biometrical comparisons of the Taurida bear with coeval European sites

Taking into account the fragmentary nature of the studied specimens we performed biplot (Fig. 5), boxplots and log ratio diagrams (Fig. 6) of selected dental elements comparing the Taurida specimens with fossil and extant ursids (Data collected from various previous publications, see Table 2 and unpublished data from authors)

The results of the bivariate plots can be seen in Figure 5: First of all, the bears of the *U*. ex. gr. *spelaeus-kanivetz* lineage always displays the largest dimensions on all the analyzed variables. On the four analyzed variables of Figure 5 (p4, m1, m2 and m3) *U. etruscus* and Pleistocene *U. arctos* displays the lower dimensions, in general the overall dimensions of *U. etruscus* are smaller as compared with *U. arctos*. Finally, the bears *U*. ex. gr. *savini-rossicus* and *U. deningeri* occupy an intermediate position between large-sized and small-sized samples. In general, the clouds of distribution of all samples overlap strongly.

p4—specifically, the overall size of this p4 are close to the average values for *U. etruscus* and *U. arctos* (Table 3). Figure 5 shows that PIN No. 5644/66 falls into the center of the area of distribution of *U. etruscus* and *U. arctos* and located in the extreme area of distribution for *U. deningeri*. Meanwhile the boxplots of Fig. 6 shows the Taurida specimen close the mean of distribution of *U. etruscus* and with clearly low values as compared with *U. deningeri* and *U. spelaeus*.

m1—The mesiodistal length and buccolingual width of m1 from Taurida Cave (PIN No. 5644/67 and No. 5644/66) are within the range of variability for *U. etruscus*, *U. deningeri*, *U*. ex. gr. *savini-rossicus*, *U*. ex. gr. *spelaeus-kanivetz* and Pleistocene *U. arctos* according to Table 3. On the contrary, Figure 5 shows the studied specimens near the center of the area of distribution for *U. arctos* and located in the extreme parts of the distribution area for *U. etruscus*, *U. deningeri* and *U*. ex. gr. *savini-rossicus*. On its turn, the boxplots of Fig. 6 display the values of Taurida specimens close to the maximum values of *U. etruscus* and Dmanisi specimens and in the lower range of cave bears.

m2—The m2 mesiodistal length and buccolingual width from Taurida Cave bears (PIN No. 5644/67; IPAE No. 727/69 and PIN No. 5644/67) show figures within the range of variability of *U. etruscus, U. deningeri*, *U*. ex. gr. *savini-rossicus* and Pleistocene *U. arctos* (Table 3). Figure 5 display a wide range of variability for Taurida specimens: PIN No. 5644/67 falls near the center distribution are for *U*. ex. gr. *savini-rossicus*; IPAE No. 727/69 close the values for *U. etruscus* and *U. arctos* and finally IPAE No. 727/69 closer to the areas of distribution of *U. etruscus*, *U*. ex. gr. *savini-rossicus* and *U. arctos*. Finally, Fig. 6 boxplots show the values of Taurida specimens just in the variability of Dmanisi sample and also close to the maximum values for *U. etruscus*.

m3—the only available m3 from Taurida (PIN No. 5644/67) have a measurements within the range of variability of this characteristic in *U. etruscus*, *U. deningeri*, *U.* ex. gr. *savini-rossicus*, *U.* ex. gr. *spelaeus-kanivetz* and Pleistocene *U. arctos* (Table 3). Meanwhile, Figure 5 display the former specimen located close to the center of the distribution area for *U. deningeri* and in the extreme parts of distribution for *U.* ex. gr. *savini-rossicus* and *U.* ex. gr. *spelaeus-kanivetz*.

Finally, the log ratios of Fig. 6 which also analyze corpus variables as longitude of the diastema, show in the first time that the Taurida specimens follow a similar patter as compared with Dmanisi, Olivola and Upper Valdarno male specimens and in second term a similar pattern of Taurida specimens as compared with *U. etruscus* from Olivola and Upper Valdarno and a quite different pattern as compared with cave bears (Fig. 6).

To sum up and as it displayed in Figures 5 and 6 the biometric analysis of the Taurida specimens as compared with Ursid fossil and extant species evidence the wide variability of the former species consequence of intraspecific variability and sexual dimorphism, however the boxplots and log ratios of Fig. 6 show the Taurida specimens close to the male representatives of *U. etruscus* from Olivola and Upper Valdarno and with close figures to the Dmanisi sample.

5.3. The comments on the relationship between the Etruscan bear and the representatives of the Taurida Cave fauna

U. etruscus co-existed with a variety of highly specialized large carnivorans, such as lynx (*Lynx issiodorensis)*, giant hyenas (*Pachycrocuta brevirostris*) and saber-toothed cats (*Homotherium* sp. and *Megantereon adroveri*). Also, the Etruscan bear had to compete with representatives of the genus *Canis* sp., the remains of which, along with felines and hyenas, were found in the Taurida Cave (Gimranov et al. 2020; Lavrov et al. 2020a, 2020b).

It’s known that early *Homo* and *P. brevirostris* (Palmqvist et al. 2011; Espigares et al. 2013; Rodríguez-Gómez et al. 2016), as well as the *Megantereon whitei* and *Homotherium latidens* were putative competitors for food resources (Martínez-Navarro and Palmqvist 1996; Arribas and Palmqvist 1999). Etruscan bear and early *Homo* were also competitors, for example, for plant resources in harsh environments (Medin et al. 2019).

The finds of the Etruscan bear in the Taurida Cave confirm the relations of the carnivorous assemblage from this locality with the dispersal of early *Homo*. This was previously stated when describing the finds of *Pachystruthio* in the Taurida Cave (Zelenkov et al.,2019). Were also noted faunistic similarities between the Tavrida and Dmanisi sites, from where the earliest Eurasian remains of *Homo* are known (Ferring et al. 2011; Lordkipanidze et al. 2013). Another worth nothing fact should be noted: there are no representatives of suids in the fauna of the Taurida Cave (Lopatin et al. 2019). Suids are also absent at Dmanisi and throughout Europe for 1.8-1.2 Ma. Researchers (Medin et al. 2019; Cherin et al. 2020) explain the absence of suids in faunas with aridification and reduction of forest biotopes, as well as with increased competition among the members of the omnivore guild (i.e., suids, ursids and hominins). Absence of suids in the fauna of Dmanisi and Taurida cave brings these two localities together and makes a closer connection of Taurida Cave fauna with the early *Homo* dispersal in Europe.

The here described finds of *U. etruscus* from Taurida Cave fauna probably marks the southernmost distribution area for this species in Eastern Europe. The Crimean peninsula is located at the junction of landscape-climatic zones, which makes these finds noteworthy in order to understand the ecological needs of the species and its morphological variability throughout the known wide distribution area.

The lower chronological boundary for the Taurida Cave deposits (ca. 1.8 Ma) is close to the boundary between the early and late evolutionary forms of the Etruscan bear. Etruscan bear was likely a typical component of eastern European faunas at the time of early *Homo* arrival. These circumstances make the new finds of the Etruscan bear from this region important for determining the evolutionary processes within the Ursidae and the historical biogeography of this period.

Conclusions

Dentognathic remains of a medium-sized ursid from Taurida Cave in Crimea are here described. The morphological variability observed in the studied specimens enabled us to include it in a early form of the species *U. etruscus* a commonly recorded species in Western Europe. The above-mentioned finds considerably expand the known geographical distribution of this species in Eastern Europe.

The chronology of the studied remains in the boundary between Middle and Late Villafranchian (ca. 1.8Ma) are roughly coeval with the earliest record of European early hominins in the geographically closer site of Dmanisi. Purported further studies in the feeding habits and ecological need of *U. etruscus* can shed light in the putative relationship of competence established between the two above-mentioned species for food resources in harsh environments.

Acknowledgements

The authors thank PE Moullé, AM Moigne, H de Lumley, E Cioppi, L Rook, S Bartolini-Lucenti, M Sotnikova, M Cherin, M Bushinadzske, D Lordkipanidze, B Martínez-Navarro and S Ros-Montoya for permits us the access to the collections under their care or for sending to us relevant literature or pictures

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by a grant of the Russian Science Foundation for young Russian scientists (project number № 20-74-00041) (DG). This work has been also funded by the Agencia Estatal de Investigación-European Regional Development Fund of the European Union (CGL2017-82654-P, AEI/FEDER-UE) and the Generalitat de Catalunya (CERCA Program). J.M.-M. is member of the consolidated research group 2017 SGR 116 (AGAUR, Generalitat de Catalunya).

References

Arribas, A. & Palmqvist, P. On the ecological connection between sabre-tooths and hominids: faunal dispersal events in the lower Pleistocene and a review of the evidence for the first human arrival in Europe. J. Archaeol. Sci. 26, 571–585 (1999).

Barlow, A. et al. Massive influence of DNA isolation and library preparation approaches on palaeogenomic sequencing data. Preprint at https://doi.org/10.1101/075911 (2016).

Barlow A., Hartmann S., Paijmans J.L.A. et al. Partial genomic survival of cave bears in living brown bears. Nature Ecology & Evolution. 2018.

Barlow, A. et al. Middle pleistocene cave bear genome calibrates the evolutionary history of palaearctic bears. SSRN Electron. J. https://doi.org/10.2139/ssrn.3523359 (2020).

Baryshnikov, G. F., & Puzachenko, A. Y. (2018). Morphometry of upper check teeth of cave bears (Carnivora, Ursidae). Boreas, 48(3), 581–604.

Baryshnikov, G. F. & Puzachenko, A. Y. : Morphometry of lower cheek teeth of cave bears (Carnivora, Ursidae) and general remarks on the dentition variability. Boreas. 2020. https://doi.org/10.1111/bor.12447. ISSN 0300-9483.

Baryshnikov, G., 2007. (Bears Family (Carnivora, Ursidae)) Semeystvo Medvezh'i (Carnivora, Ursidae). Fauna Rossii i sopredel'nykh stran (in Russian). Nauka, St. Petersburg (541 p.).

Baryshnikov, G. Middle Pleistocene Ursus thibetanus (Mammalia, Carnivora) from Kudaro caves in the Caucasus // Proceeding of the Zoological Institute RAS, 2010. Vol. 314. N 1. P. 67-79.

Boeskorov G.G., Grigoriev S.E., Baryshnikov G.F. 2012. New Evidence for the Existence of Pleistocene Cave Bears in Arctic Siberia // Doklady Biological Sciences 445(1):239-243.

Boeskorov G.G., Baryshnikov G.F. 2013. Late Quaternary carnivora of Yakutia. Editor-in-Chief A.V. Abramov. (in Russian). Nauka, St. Petersburg (199 p.).

Borissiak, A., 1932. (New race of cave bear from the Quaternary deposits of Northern Caucasus). Novaya rasa peshchernogo medvedya iz chetver-tichnykh otlozheniy Sev. Kavkaza (in Russian). Trudy Paleozoolog.Inst. 1, 137–201.

Cherin, M., Alba, D. M., Crotti, M., Menconero, S., Moullé, P. É., Sorbelli, L., & Madurell-Malapeira, J. (2020). The post-Jaramillo persistence of Sus strozzii (Suidae, Mammalia) in Europe: new evidence from the Vallparadís Section (NE Iberian Peninsula) and other coeval sites. *Quaternary Science Reviews*, *233*, 106234.

Crégut-Bonnoure E., 1996. A review of small Middle Pleistocene bears from France // Acta Zoologica Cracoviensis. V. 39. № 1. P. 89–101.

Dehm R., 1943. Ein besonders kleiner Bär (Ursus schertzi n. sp.) aus dem Löß von Achenheim bei Straßburg im Elsaß // Neues Jahrbuch für Mineralogie, Geologie und Paläontologie. B. P. 137–153.

Erdbrindk, P., 1953. A review of fossil and recent bears of the Old Worldwith remarks on their phylogeny based on their dentition. Jan deLange, Deventer, Netherlands (597 p.).

Espigares, M. P. et al. Homo vs. Pachycrocuta: earliest evidence of competition for an elephant carcass between scavengers at Fuente Nueva-3 (Orce, Spain). Quat. Int. 295, 113–125 (2013).

Fistani A., Crégut-Bonnoure E., 1993. Découverte d'Ursus thibetanus (Mammalia, Carnivora, Ursidae) dans le site pléistocéne moyen de Gajtan (Shkoder, Albanie) // Geobios. V. 26. P. 241–263.

Frischauf C., Nielsen E., Rabeder G. 2017. The cave bears (Ursidae, Mammalia) from Steigelfadbalm near Vitznau (Canton of Lucerne, Switzerland). Acta zool. cracov., 60(2): 35-57.

García, N., Arsuaga, J.L., 2001. Ursus dolinensis: a new species of Early Pleistocene ursid from Trinchera Dolina, Atapuerca (Spain). C. r. Acad. Sci. Paris. Sér. Sci. Terre Planètes. 332, 717–725.

García Vázquez A., 2015. Caracterización del oso pardo (Ursus arctos L.) fósil en el NW de la Península Ibérica: datos morfométricos y moleculares (Unpublished Ph. D. Thesis). Universidade da Coruña. Instituto Universitario de Xeoloxía: Spain.

Gibbard, P.L., Head, M.J., Walker, M.J.C., 2010. Formal ratification of theQuaternary System/Period and the Pleistocene Series/Epoch with abase at 2.58 Ma. J. Quat. Sci. 25 (2), 96–102.

Gimranov D.O., 2018. Morphotypic characteristics of the fourth premolars of the brown (Ursus arctos) and polar (Ursus maritimus) bears (Carnivora, Ursidae) // Zoological Journal. V. 97, № 2, P. 205–223.

Gimranov D.O., Lavrov A.V., Startsev D.B., et al. First finding of Etruscan bear (Ursus etruscus, Ursidae, Carnivora) in the Crimea (Taurida cave, Early Pleistocene). Doklady Biological Sciences. 2020; 491:35–38. doi: 10.1134/S0012496620020040

Gimranov D.O. New data on Ursus (Euarctos) thibetanus G. Cuvier 1823 (Carnivora, Ursidae) of the Pleistocene Urals // Zoological Journal, 2019, V. 98, № 10, P. 1168–1176.

Jiangzuo Q., Liu J., Wang Y., Jin C., Liu S., Liu J., Chen J. New materials of Ursus etruscus from Jinyuan cave of Luotuo hill, Dalian and a brief review of Ursus cf. etruscus in china // Quatern. Sci. 2017. V. 37. № 4. P. 828–837.

Jiangzuo, Q., Wagner, J., Chen, J., Dong, C., Wei, J., Ning, J., & Liu, J. 2018. Presence of the middle Pleistocene cave bears in China confirmed–Evidence from Zhoukoudian area. *Quaternary Science Reviews*, *199*, 1-17.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4, 1-9.

Hofreiter, M., Münzel, S., Conard, N.J., Pollack, J., Slatkin, M.,Weiss, G., Pääbo, S., 2007. Sudden replacement of cave bear mitochondrial DNA in the late Pleistocene. Curr Biol 17:R122.

Koufos, G.D., Konidaris, G.E., Harvati, K., 2017. Revisiting Ursus etruscus (Carnivora, Mammalia) from the Early Pleistocene of Greece with description of new material. Quat. Int. 497, 222–239.

Knapp M. 2019. From a molecules' perspective – contributions of ancient DNA research to understanding cave bear biology. Historical Biology 31: 442–447.

Knapp M, Rohland N, Weinstock J, et al. 2009. First DNA sequences from Asian cave bear fossils reveal deep divergences and complex phylogeographic patterns. Molecular Ecology 18: 1225–1238.

Krause, J., Unger, T., Noçon, A., Malaspinas, A.-S., Kolokotronis, S.-O., Stiller, M., Soibelzon, L., Spriggs, H., Dear, P. H., Briggs, A. W., Bray, S. C. E., O'Brien, S. J., Rabeder, G., Matheus, P., Cooper, A., Slatkin, M., Pääbo, S., Hofreiter, M. (2008): Mitochondrial genomes reveal an explosive radiation of extinct andextant bears near the Miocene-Pliocene boundary. – BMC Evolutionary Biology, 8: 220 (12 pp.).

Kurtén, B., Crusafont-Pairó, M., 1977. Villafranchian carnivores (Mammalia) from La Puebla de Valverde (Teruel, Spain) Comm. Biologicae, 85 (1977), pp. 1-39

Lavrov A.V., Tarasenko K.K., Gimranov D.O. et al. The saber-toothed cats (Carnivora, Felidae, Machairodontinae) from the Lower Pleistocene of Taurida cave, Crimea // DAN. 2020a. (in press).

Lavrov A.V., Gimranov D.O., Startsev D.B. et al. Pachycrocuta brevirostris of Taurida cave, Crimea // DAN. 2020b. (in press).

Lopatin A.V., Vislobokova I.A., Lavrov A.V., et al. The Taurida Cave, a new locality of Early Pleistocene vertebrates in Crimea. Doklady Biological Sciences. 2019; 485:40–43. doi: 10.1134/S0012496619020066

Lopatin A.V. The coocurence of Hypolagus and Lepus (Leporidae, Lagomorpha) in the Early Pleistocene of Crimea. Doklady Biological Sciences. 2019a; 489 (6): 651–653. doi: 10.1134/S0012496619020066

Lopatin A.V. The Porcupine Hystrix (Acanthion) vinogradovi (Rodentia, Hystricidae) from the Early Pleistocene Taurida locality in Crimea. Doklady Biological Sciences. 2019b; 486 (6): 756–762. doi: 10.1134/S0012496619020066

Lordkipanidze D., Ponce de León M.S., Margvelashvili A., Rak Y., Rightmire G.P., Vekua A., Zollikofer C.P.E. A Complete Skull from Dmanisi, Georgia, and the Evolutionary Biology of Early Homo / Science 342, 326-331 (2013); DOI: 10.1126/science.1238484

Madurell-Malapeira, J., Minwer-Barakat, R., Alba, D. M., Garcés, M., Gómez, M., Aurell-Garrido, J., Moyà-Solà, S. & Berástegui, X. (2010). The Vallparadís section (Terrassa, Iberian

Peninsula) and the latest Villafranchian faunas of europe. *Quaternary Science Reviews*, *29*(27-28), 3972-3982.

Madurell-Malapeira, J., Ros-Montoya, S., Espigares, M. P., Alba, D. M., & Aurell-Garrido, J. (2014). Villafranchian large mammals from the Iberian Peninsula: paleobiogeography, paleoecology and dispersal events. *Journal of Iberian Geology*, *40*(1), 167-178.

Madurell-Malapeira, J., Bartolini-Lucenti, S., Prat-Vericat, M., Sorbelli, L., Blasetti, A., Ferreti, M., Goro, A., & Cherin, M. (2021, published online). Jaramillo-aged carnivorans from Collecurti (Colfiorito Basin, Italy). *Historical Biology*

Martínez-Navarro, B. & Palmqvist, P. Presence of the African Saber-toothed Felid Megantereon whitei (Broom, 1937) (Mammalia, Carnivora, Machairodontinae) in Apollonia-1 (Mygdonia Basin, Macedonia, Greece). J. Archaeol. Sci. 23, 869–872 (1996).

Mazza, P., Rustioni, M., 1992. Morphometric revision of the Eurasian species Ursus etruscus Cuvier. Palaeontogr. Ital. 79, 101-146.

Mazza, P., Rustioni, M., 1994. On the phylogeny of Eurasian bears. Palaeontogr. Abt. A 230, 1-38.

Medin, T. et al. Late Villafranchian Ursus etruscus and other large carnivorans from the Orce sites (Guadix-Baza Basin, Andalusia, Southern Spain): Taxonomy, biochronology, paleobiology, and ecogeographical context. Quat. Int. 431, 26–42 (2017).

Medin, T., Martínez-Navarro, B., Madurell-Malapeira, J., Figueirido, B., Kopaliani, G., Rivals, F., Kiladze, G., Palmqvist, P., Lordkipanidze, D., 2019. The bears from Dmanisi and the first dispersal of early Homo out of Africa. Sci. Rep. 9:17752 | https://doi.org/10.1038/s41598-019-54138-6

Moigne, A. M., Palombo, M. R., Belda, V., Heriech-Briki, D., Kacimi, S., Lacombat, F. & Testu, A. (2006). Les faunes de grands mammifères de la Caune de l'Arago (Tautavel) dans le cadre biochronologique des faunes du Pléistocène moyen italien. *L'anthropologie*, *110*(5), 788-831.

Monchot, H., M. Mashkour, F. Biglari, and K. Abdi. 2019. The upper pleistocene brown bear (Carnivora, Ursidae) in the Zagros: evidence from Wezmeh Cave, Kermanshah, Iran. Annales de Paléontologie: In Press. doi: 10.1016/j.annpal.2019.102381

Mottl M. (1964) Bärenphylogenese in Südost-Österreich. Mitteilung des Museums für Bergbau, Geologie und Technik am Landesmuseum “Joanneum” 26, 1–56.

Moullé, P. E. Les grands mammifères du Pléistocene inférieur de la grotte du Vallonnet (Roquebrunne, Cap Martín, Alpes Maritimes). Étude paléontologique des Carnivores, Equidae, Suidae et Bovidae (Unpubl. Ph.D. Dissertation, 1992).

Musil, R. 1972. Die Bären der Stranska Skala. Anthropos 20, 107–111.

Musil, R. 1991. Die Bären von Bilzingsleben. Bilzingsleben IV. In Fischer, K., Guenther, E.W., Heinrich, W.-D., Mania, D., Musil, R. & Nötzold, T. (eds) Homo erectus – seine Kultur und seine Umwelt. Veröffentlichungen des Landesmuseums für Vorgeschichte in Halle 44. P. 81-102.

Musil, R., 2001. Die Ursiden-Reste aus dem Unterpleistozan von Untermassfeld. In: Kahlke, R.D. (Ed.), Das Pleistozan von Untermassfeld bei Meiningen (Thüringen), Teil 2. Monographien des Romisch-Germanischen Zentralmuseums Mainz 40, 2. P. 633-658.

Musil, R. (2005). Die Bärenpopulation von Bilzingsleben – eine neue mittelpleistozäne Art. Munibe (Antropologia-Arkeologia), 57/1, 67–101.

Nomade S., Pastre J.F., Guillou H. et al. 40Ar/39Ar constraints on some French landmark Late Pliocene to Early Pleistocene large mammalian paleofaunas: Paleoenvironmental and paleoecological implications // Quatern. Geochron. 2014. V. 21. P. 2–15.

Quilès, J. 2003. Les Ursidae du Pléistocène moyen et supérieur en Midi méditerranéen: Apports paléontologiques, biochronologiques et archéozoologiques. (Unpublished Ph. D. Thesis). Muséum National d'Histoire Naturelle: Paris.

Oksinenko P.V., Lavrov A.V. Geomorphological characteristics and reconstruction of the history of the formation of the cave "Taurida" (Belogorsky district, Crimea) // Herald of MSU. Ser. Geograph. 2020. (in press). [In Russian with English summary]

Pacher, M., 2007. The type specimen of Ursus priscus Goldfuss, 1810 and the uncertain status of Late Pleistocene brown bears. Neues Jahrbuch Geol. Palaontol. Abhand. 245, 331–339.

Pacher, M. (2017): Anterior premolar variability in Pleistocene cave and brown bears and its significance in species determination. – Fossil Imprint, 73(3-4): 482–494, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Palmqvist, P. et al. The giant hyena Pachycrocuta brevirostris: modelling the bone-cracking behavior of an extinct carnivore. Quat. Int. 243, 61–79 (2011).

Pei W., 1934. On the Carnivora from Locality 1 of Choukutien // Palaeontologia Sinica. V. 8. P. 1–217.

Petrucci, M., Cipullo, A., Martínez-Navarro, B., Rook, L., Sardella, R., 2013. The late Villafranchian (early Pleistocene) carnivores (Carnivora, mammalia) from Pirro Nord (Italy). Palaeontogr. A 298, 113-145.

Petrucci M., Sardella R., 2009. Ursus etruscus Cuvier, 1823 from the Early Pleistocene of Monte Argentario (Southern Tuscany, Central Italy) // Bollettino della Società Paleontologica Italiana (nl), Modène, Società Paleontologica Italiana, vol. 48, no 2, P. 89-94.

Prat-Vericat, M., Rufí, I., Llenas, M. et al. Middle Pleistocene Ursus deningeri from Grotte de la Carrière (Réseau Lachambre, Têt Valley, Eastern Pyrenees). J Iber Geol (2020). https://doi.org/10.1007/s41513-020-00124-1

Rabeder, G., Pacher, M., Withalm, G., 2010. Early Pleistocene bear remains from Deutsch-Altenburg (Lower Austria). Mitt. Komm. Quartärkomm. Österr. Akad. Wiss. 17, 1–135.

Rabeder, G., Frischauf, C., Pacher, M., 2016. A new reference of Ursus deningeroides in Lower Austria. Cranium 33, 8–13.

Riek G., 1973. Das Paläolithikum der Brillenhöhle bei Blaubeuren (Schwäbische Alb). Teil I. Forsch. u. Ber. z. Vor-und Frühgesch. in Baden-Württemberg 4/I. Stuttgart. pp. 168.

Rodríguez-Gómez, G. et al. On the ecological context of the earliest human settlements in Europe: Resource availability and competition intensity in the carnivore guild of Barranco León-D and Fuente Nueva-3 (Orce, Baza Basin, SE Spain). Quat. Sci. Rev. 143, 69–83 (2016).

Sabol, M. 1998: The cave bear (Ursus spelaeus Rosenmüller et Heinroth) from the Tmavá skala cave. Mineralia Slovaca, 30, 285-308.

Sharapov, Sh., 2014. Late Cenosoic mammalian fauna of South-East middle Asia. Fauna of Republic Tajikistan. V.1. N.1. The carnivore mammals (order Carnivora). Publishing house «Donish». Dushanbe (363 p.).

Soergel, W., 1925. Die Säugetierfauna des altdiluvialen Tonlagers Ton Jockgrim in der Pfalz. Zeitschrift der Deutschen Geologischen Gesellschaft Band 77, p. 405 - 438.

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.

Stiller, M. et al. diversity and evolution of the Pleistocene cave bear complex. Quaternary International 339–340, 224–231, https:// doi.org/10.1016/j.quaint.2013.09.023 (2014).

Torres, T. 1984. Úrsidos del Pleistoceno-holoceno de la Península Ibérica (Unpublished Ph. D. Thesis). Escuela Técnica Superior de Ingenieros de Minas: Madrid.

Tsoukala E., Bonifay M.-F. 2004. The Early Pleistocene Carnivores (Mammalia) from Ceyssaguet (Haute-Loire). Paleo, 16: 193-242.

Viret, J. Le loess â banks durcis de Sainte-Vallier (Drôme) et sa faune de mammaiferes villafranchiens. Mus. Hist. Nat. Nouv. Arch. 4, 1–200 (1954).

Vislobokova I.A., Titov V.V., Lavrov A.V., et al. Early Pleistocene Spiral-Horned Antelopes (Artiodactyla, Bovidae) from the Taurida Cave (Crimea, Russia). Paleontological Journal. 2020; 54(1):81–90. doi: 10.1134/S0031030120010116

Vislobokova I.A., Titov V.V., Lavrov A.V., Startsev D.B., Tarasenko K.K., Lopatin A.V. 2019. On the occurrence of giant deer of the genus Arvernoceros at Taurida Cave in Crimea // Doklady Biological Sciences. 2020; 487 (5): 596-599. doi: 10.1134/S0012496619020066

Wagner, J., Cermak, 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. Bull. Geosci. 87, 461–496.

Wagner J., Jiangzuo Q., Lenardić J.M., Liu J., 2017. Taxonomic revision of bears from the locality Šandalja i (Croatia) and its biostratigraphic consequences // Fossil Imprint. V. 73. № 3–4. P. 533–544.

Zapfe, H., 1948. Die altplistozänen Bären von Hundsheim in Niederösterreich. — Jb. Geol. Bundesanstalt, 1946 (3-4):95–164, Wien.

Zelenkov N.V., Lavrov A.V. Startsev D.B., Vislobokova I.A., Lopatin A.V. 2019. A giant early Pleistocene bird from Eastern Europe: unexpected component of terrestrial faunas at the time of early Homo arrival // Journal of Vertebrate Paleontology: e1605521. Pp. 1-7. https://doi.org/10.1080/02724634.2019.1605521

Figure captions

Figure 1. Geographical location of the Taurida Cave within the Crimean peninsula dn topography of the cave (Modified from Zelenkov et al. 2019).

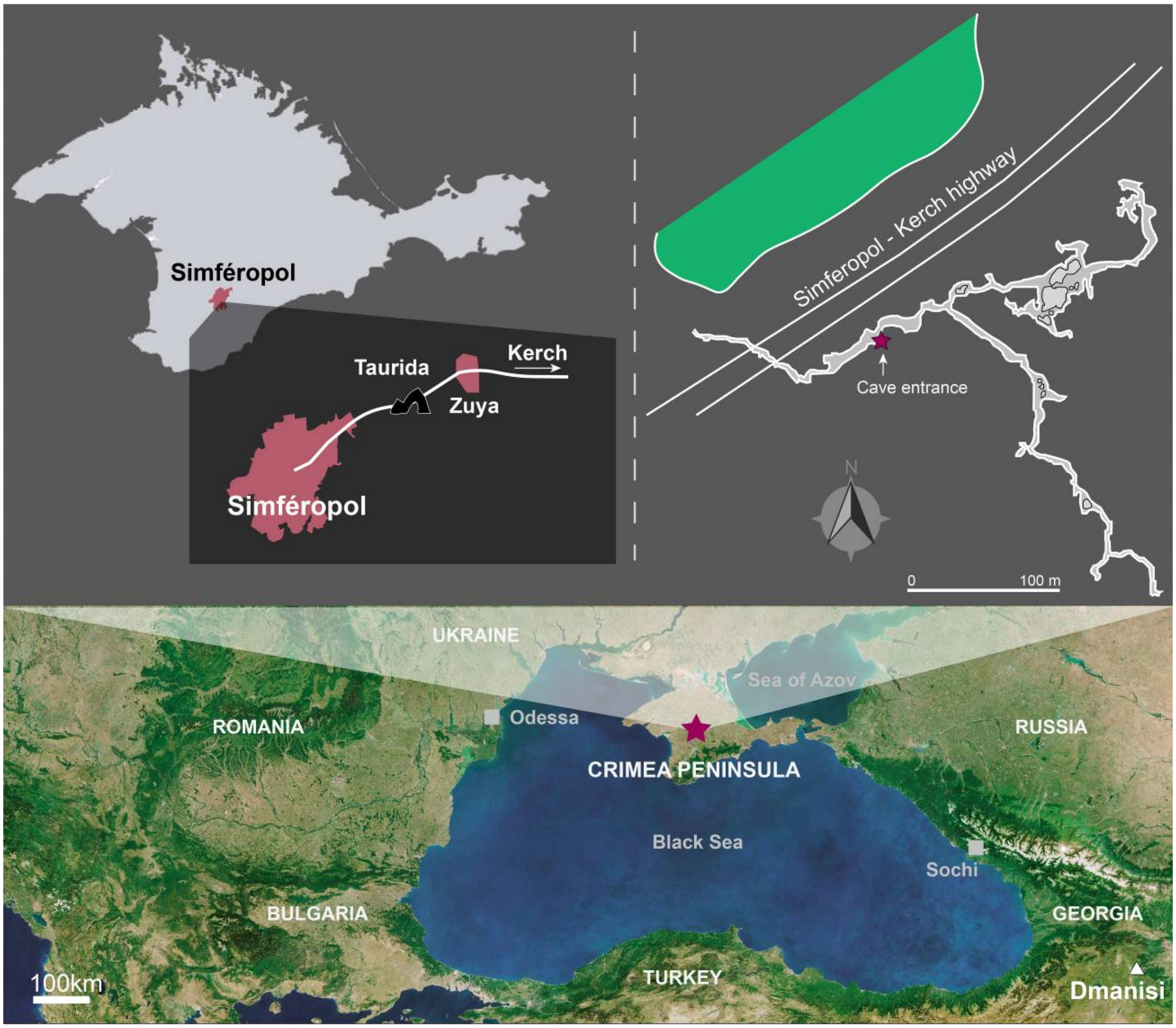

Figure 2. Dentognathic specimens of *Ursus etruscus* from Taurida Cave. PIN No. 5644/67 fragment of left corpus with m1-m3 in A, buccal B, lingual and C occlusal views. PIN No. 5644/66 partial left and right corpora with right p4-m1 in D left buccal E occlusal and F right buccal views. IPAE No. 727/69 right m2 in G buccal H occlusal and I lingual views.

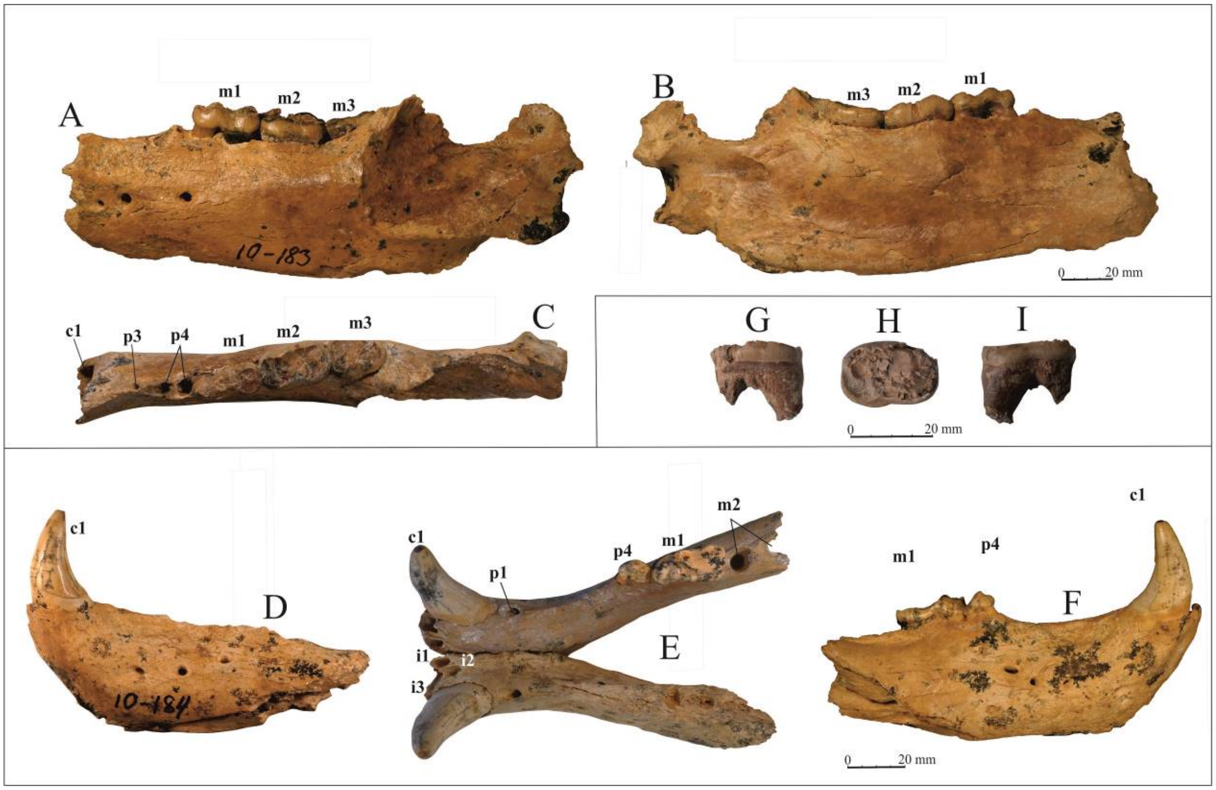

Figure 3. Corpora of Early Pleistocene *Ursus* species in buccal view. A-H *Ursus etruscus*: A Kuruksay (Russia, ca. 2.2. Ma) left corpus nº 3120-701; B Olivola (Italy, ca. 2.0 Ma) left corpus IGF4595; C Upper Valdarno (Italy, ca. 1.8Ma) left corpus IGF905; D Dmanisi (Georgia, ca. 1.8 Ma) left corpus D4940; E Taurida Cave (Russia, ca. 1.8-1.5 Ma) left corpus PIN No. 5644/67; F Taurida Cave (Russia, ca. 1.8-1.5 Ma) right corpus PIN No. 5644/66; G Pietrafitta (Italy, ca. 1.6-1.4 Ma) right corpus without number; H Fuente Nueva 3 (Spain, ca. 1.3 Ma) right corpus FN302 U96 N9 . I *Ursus deningeri* from Vallonnet Cave (France, ca. 1.2 Ma) right corpus C8 C112 2172.

Figure 4. First lower molars of *U. etruscus* compared with of other Pleistocene members of the genus *Ursus* (occlusal view). A-E: *U. etruscus*, F-J: Cave bears, K-N: *U. arctos*. A Kuruksay left m1 nº 3120-701; B Olivola left m1 IGF4595; C Dmanisi left m1 D4940; D Venta Micena (Spain, ca.1.5 Ma) right m1 VM10318; E Taurida PIN no 5644/67. F Vallonnet left m1 C8 C112 2172; G Aragó Cave (*U. deningeri*, France, ca. 0.5 Ma) left m1 G13 GEP22 1112; H Grotte de la Carrière (*U. deningeri*, France; ca. 0.3 Ma) left m1 GDC15-D6-34-Nv4; I Mishin Kamik (*U.* ex. gr. *savini-rossicus*, Bulgaria) left m1 FM 3376; J Goyet Cave (*U.* ex. gr. *spelaeus-kanivetz* , Belgium) right m1 RBINS 2170. K Kudaro 3 (South Ossetia) left m1 ZIN 34595 ; L Zhilische Sokola Cave right m1 IPAE 802/1338 ; M Severnaya Cave left m1 IPAE 2079/241 and N left m1 NHM O.C.1. Scale bar equals 1 cm.

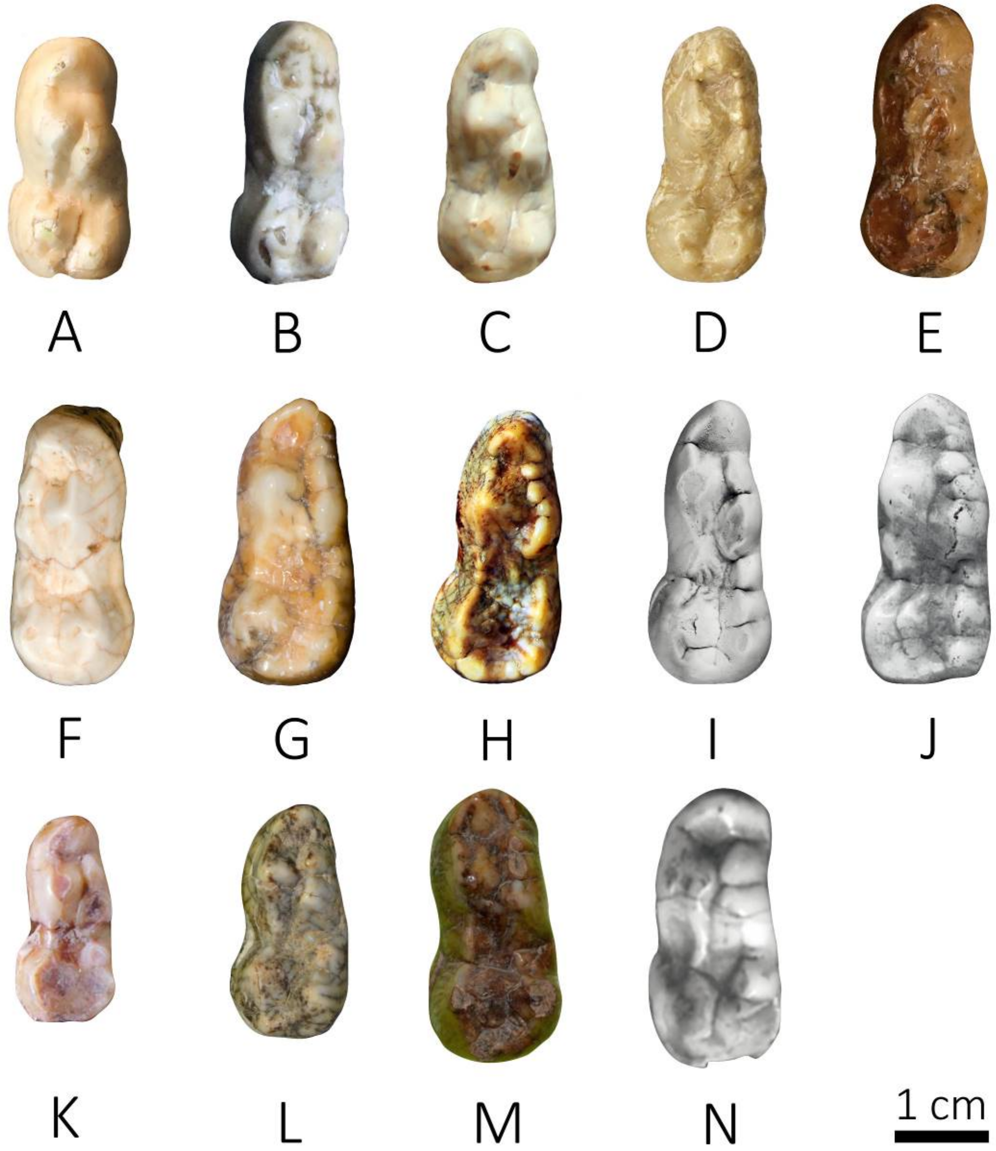

Figure 5. Biplots of mesidistal length versus buccolingual width of selected teeth of extant and fossil *Ursus* species.

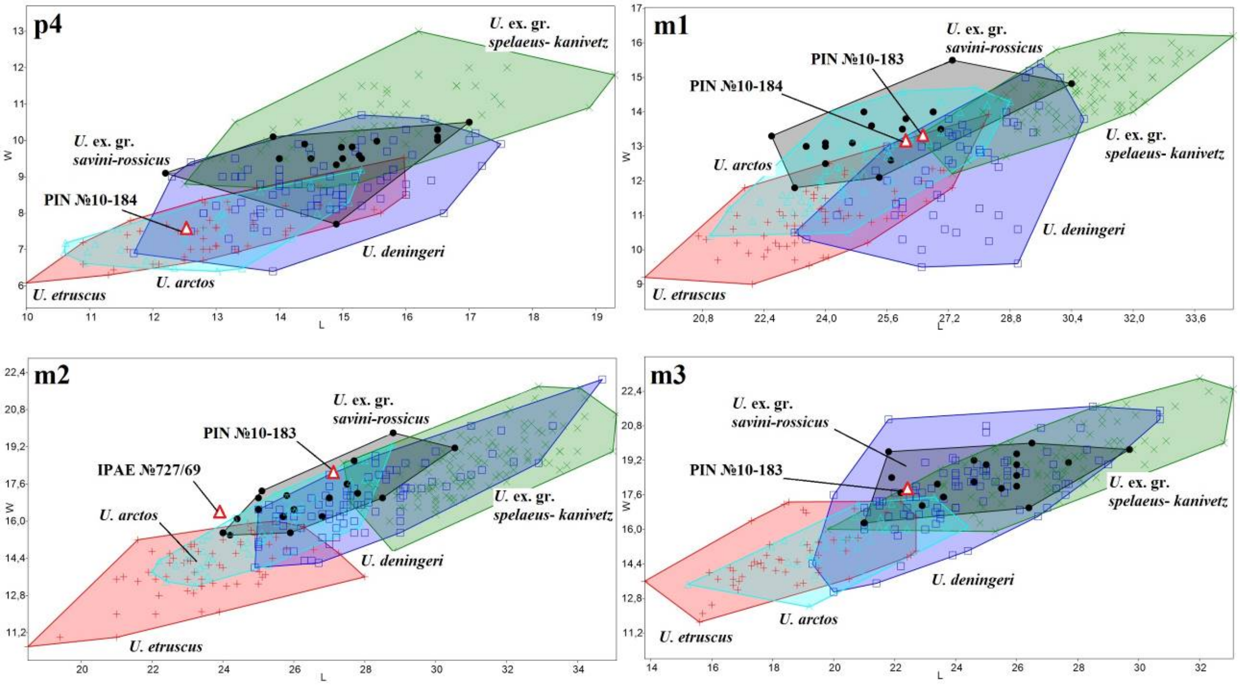

Figure 6. Boxplots of selected dental elements on Pleistocene and living *Ursus* species on the top and logratios of dentognathic variables comparing the Taurida sample with fossil bear specimens form coeval localities.

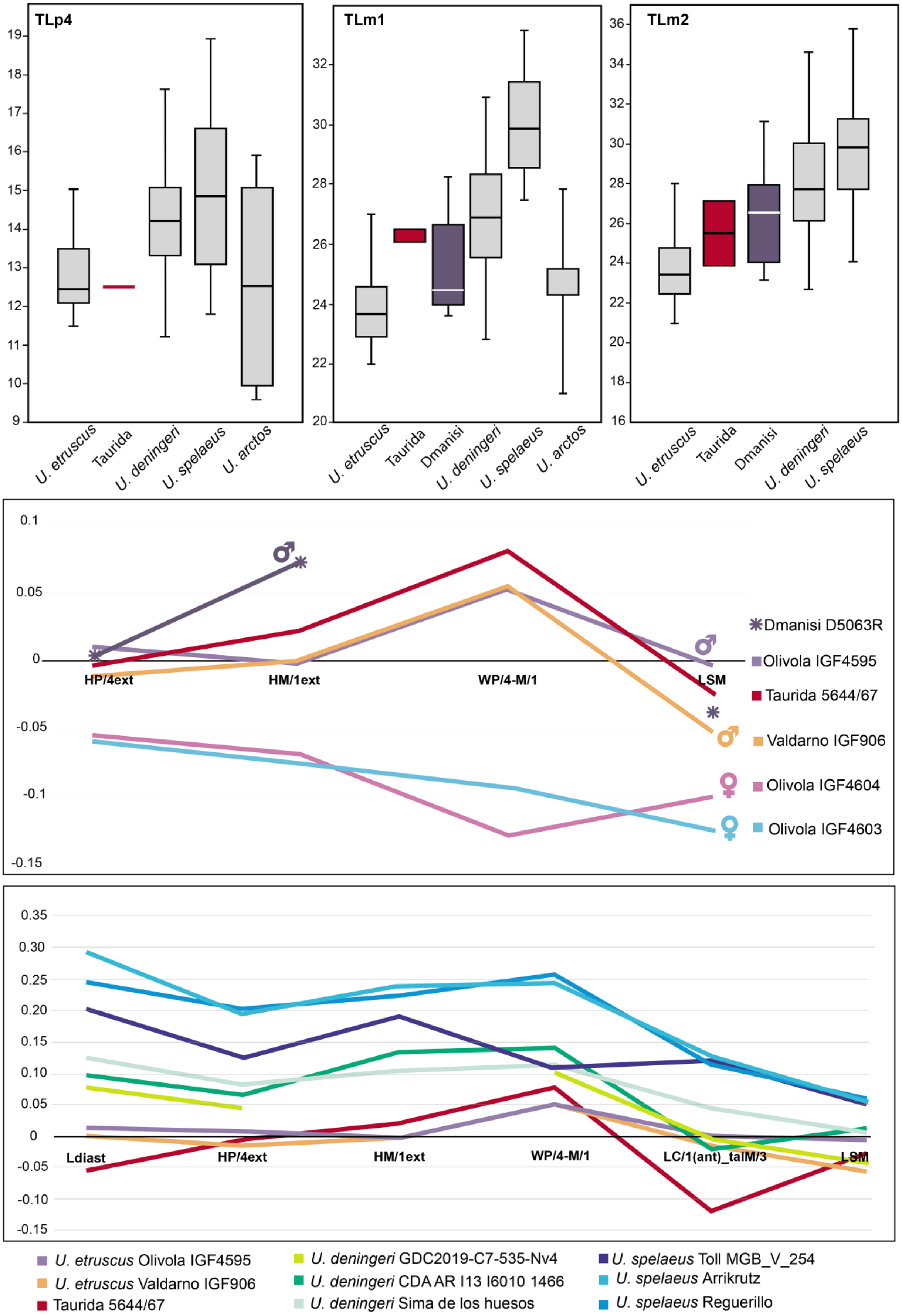
TLp4
9
10
11
12
13
14
15
16
17
18
19
U. etruscus
Taurida
U. deningeri
U. spelaeus
U. arctos
TLm1
20
22
24
26
28
30
32
U. etruscus
Taurida
Dmanisi
U. deningeri
U. spelaeus
U. arctos
TLm2
16
18
20
22
24
26
28
30
32
34
36
U. etruscus
Taurida
Dmanisi
U. deningeri
U. spelaeus
0.1
0.05
0
-0.05
-0.1
-0.15
HP/4ext
HM/1ext
WP/4-M/1
LSM
♂
♂
♂
♀
♀
✱Dmanisi D5063R
■Olivola IGF4595
■ Taurida 5644/67
■ Valdarno IGF906
■ Olivola IGF4604
■ Olivola IGF4603
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0
-0.05
-0.10
-0.15
Ldiast
HP/4ext
HM/1ext
WP/4-M/1
LC/1(ant)_talM/3
LSM
■ U. etruscus Olivola IGF4595
■ U. etruscus Valdarno IGF906
■ Taurida 5644/67
■ U. deningeri GDC2019-C7-535-Nv4
■ U. deningeri CDA AR I13 I6010 1466
■ U. deningeri Sima de los huesos
■ U. spelaeus Toll MGB_V_254
■ U. spelaeus Arrikrutz
■ U. spelaeus Reguerillo

Table 1. Measurements of *U. etruscus* from Taurida cave.

Measurements	PIN No. 5644/67	PIN No. 5644/66**	IPAE No. 727/69
L diastema	19.8*	35.7	-
L c1-m3	119.7*	-	-
L p4-m3	92.5*	-	-
L m1-m3	77.1	-	-
H diastema	49.8	41.6	-
H below p4	51.3	46.5	-
H below m1	52.7	-	-
W below m1	21.3	-	-
L c1	-	21.2	-
W c1	-	14.0	-
L p4	-	12.5	-
W p4	-	7.5	-
L m1	26.5	26.1	-
W m1	13.3	13.2	-
L m2	27.1	-	23.9
W m2	18.1	-	16.4
L m3	22.4	-	-
W m3	17.9	-	-

* the alveolus is broken, ** measurements along the right ramus of the lower jaw

Table 2. Published data on different representatives of Ursidae inhabiting the territory of Eurasia in the Pleistocene used in this study

Species	Locality	Geography	Published data
U. thibetanus	Azykh	Azerbaijan	Baryshnikov 2007
	Mauer	Germany	
	Miyata	Japan	
	Perpignan	France	
	Kudaro 1	Russia	Baryshnikov 2010
	Laaerberg	Austria	
	Cedres cave	France	Crégut-Bonnoure 1996
	Aldene		
	Balarus VII		
	Orgnac 3		
	Reale		
	Cimay	France	Fistani and Crégut-Bonnoure 1993; Crégut-Bonnoure 1996; Baryshnikov 2007
	Gajtan	Albany	Fistani and Crégut-Bonnoure 1993
	Achenheim	France	Dehm 1943; Fistani and Crégut-Bonnoure 1993
	Zhoukoudian 1	China	Pei 1934
	Imanay	Russia	Gimranov 2019
	Šandalja I	Croatia	Wagner et al. 2017
U. etruscus	Jinyuan cave	China	Jiangzuo et al. 2017
	Laochihe		
	Zhoukoudian Loc.18		
	Ceyssaguet	France	Tsoukala and Bonifay 2004
	Kuruksay	Tajikistan	Baryshnikov 2007
	Olivola	Italy	Mazza and Rustioni 1992
	Pietrafitta		
	Senèze	France	
	Pirro Nord	Italy	Mazza and Rustioni 1992; Petrucci et al. 2013
	Saint-Vallier	France	Mazza and Rustioni 1992; Baryshnikov 2007
	Upper Valdarno	Italy	
	Monte Argentario	Italy	Petrucci and Sardella 2009
	Tsiotra Vryssi (TSR)	Greece	Koufos et al. 2017
	Tegelen, Netherlands	Netherlands	Erdbrink 1953; Viret,1954
	Fuente Nueva-3	Spain	Medin et al. 2017
	Barranco León		
	Venta Micena		
	Dmanisi	Georgia	Medin et al. 2019
U. deningeri	Bilzingsleben	Czech Republic	Musil 1991; Musil 2005
	Stránská skála	Czech Republic	Musil 1972
	Caune de l'Arago	France	Quilés 2003
	Gargas	France	Baryshnikov 2007
	Steinheim	Germany	
	Subenborn		
	Untermassfeld		
	Grotte de la Carrière Sondage 1	France	Prat-Vericat et al. 2020
	Mosbach	Germany	Soergel 1925; Zapfe 1948

	Šandalja I	Croatia	Wagner et al. 2017
	Vallonnet	France	Moullé 1992
U. dolinensis	Atapuerca TD	Spain	Garcia and Arsuaga 2001
U. deningeroides	Dripstone cave of Flatz	Austria	Rabeder et al. 2016
	Repolust	Austria	Mottl 1964
U. ex. gr. *savini-rossicus*	Krasnodar	Russia	Borissiak 1932
	Bachatsk		Baryshnikov 2007
	Berezhekovo		
	Kudaro 1		
	Mohovo		
	Red Yar on the Ob River		
	Ulahan Sullar		Boeskorov et al. 2012
	Mishin Kamik	Bulgaria	Spassov et al. 2017
U. ex. gr. *spelaeus-kanivetz*	Steigelfadbalm	Switzerland	Frischauf et al. 2017
	Arbreda	Spain	Quilés 2003
	Crouzade	France	
	Hortus		
	Portel		
	Tournal		
	Brillenhohle	Germany	Riek 1973
	Tmava skala	Slovakia	Sabol 1998
	Cova d'Erinya	Spain	Torres 1984
	Cueva de Aizkitri		
	Cueva de El Castillo		
	Cueva de Gaztelo		
	Cueva de la Lastrilla II		
	Cueva de Las Monedas		
	Cueva de Las Tuxoneras		
	Cueva de Los Casares		
	Cueva de Urnieta		
	Cova Gran		
	Raclau Viver		
	Sima de Ekain		
U. arctos	A Valiña	Spain	Gárcia Vázquez 2015
	La Canal Fuerte		
	O Eixe		
	Pena Paleira (Alta)		
	Pozu La Cigacha		
	Purruñal		
	Somiedo		
	Tarelo		
	Wezmeh cave	Iran	Monchot et al. 2019
	Orgnac III	France	Quilés 2003
	Deutsch-Altenburg 4	Austria	Rabeder et al. 2010
	Cueva FC-20	Spain	Torres 1984
	Cueva de Aketegui		
	Cueva de Ekain		
	Cueva de la Bodega		
	Cueva de la Corta		
	Cueva de la Fuente		
	Cueva de la Sierra dos Molianos		
	Cueva de Las Figuras		
	Cueva de Las Tuxoneras		
	Cueva de Los Casares		
	Cueva de Putxerri		

	Cueva de Troskaeta		
	Cueva Noruega		
	Grota das Fontainhas		
	Sima de la Cuna		
	Sima de Los Grajas		
	Sima T-20		
	Sima Tresviso		
	Urkizetako Koba		
	Bolshaya Chukchya River	Russia	Boeskorov and Baryshnikov 2013
	Kyra-Sullar		
	Mamontova Gora		
	Oshbordoh		
	Kudaro 3	Russia	Baryshnikov 2010
	Eliseevichi		
	Aman-Kutan	Uzbekistan	
	Genista Cave	Gibraltar	
	Koneprusy	Czech Republic	
	Predmosti		
	Monte Verde	Italy	
	Taubach	Germany	
	Chatillon-Saint-Jeans	France	Baryshnikov 2007
	Ingarano	Italy	

Table 3. Length (L) and width (W) of teeth of the Ursidae that inhabited the territory of Eurasia in Pleistocene.

Name of measure		***U. thibetanus***	***U. etruscus***	***U. deningeri***	***U.* ex. gr. *savini-rossicus***	***U.* ex. gr. *spelaeus-kanivetz***	***U. arctos***	***U. etruscus* PIN No. 5644/67**	***U. etruscus* PIN No. 5644/66**	***U. etruscus* IPAE No. 727/69**
***L* p4**	**Lim**	8.9-12.1	10.0-16.0	11.7-17.5	12.2-17.0	12.5-19.3	10.6-15.3	-	-	-
	Mean	10.5	13.0	14.6	15.1	15.5	12.9	-	12.5	-
	n	11	52	79	19	57	35	-	1	-
***W* p4**	**Lim**	5.8-7.7	6.1-9.5	6.4-10.7	7.7-10.5	8.7-13.0	6.4-9.2	-	-	-
	Mean	6.4	7.5	8.8	9.6	10.5	7.5	-	7.5	-
	n	11	52	79	19	57	35	-	1	-
***L* m1**	**Lim**	18.8-22.3	19.3-28.2	23.2-30.7	22.6-30.4	26.4-34.6	21.0-28.8	-	-	-
	Mean	20.6	23.8	27.4	25.5	30.6	24.7	26.5	26.1	-
	n	13	63	56	20	93	68	1	1	-
***W* m1**	**Lim**	8.6-10.8	9.0-13.9	10.3-15.4	11.8-15.5	12.2-16.3	10.4-14.7	-	-	-
	Mean	9.7	11.0	12.7	13.4	14.5	12.4	13.3	13.2	-
	n	13	63	56	20	93	68	1	1	-
***L* m2**	**Lim**	19.3-23.1	18.5-28.0	24.9-34.7	24.0-30.5	27.4-35.1	22.0-28.8	-	-	-
	Mean	21.0	23.6	28.1	26.4	31.1	25.1	27.1	-	23.9
	n	12	64	84	21	115	52	1	-	1
***W* m2**	**Lim**	11.0-14.2	10.6-16.0	14.0-22.1	15.4-19.8	14.7-21.8	13.2-19.3	-	-	-
	Mean	12.5	14.0	16.9	17.0	18.4	15.6	18.1	-	16.4
	n	12	64	84	21	115	52	1	-	1
***L* m3**	**Lim**	14.2-19.2	13.8-22.7	19.3-30.7	21.0-29.7	19.8-33.1	15.2-24.4	-	-	-
	Mean	16.2	18.7	24.4	24.8	27.4	20.4	22.4	-	-
	n	14	52	90	20	83	40	1	-	-
***W* m3**	**Lim**	8.9-14.8	11.7-17.3	13.1-21.7	16.3-20.0	15.9-23.0	12.4-17.5	-	-	-
	Mean	12.1	14.7	17.8	18.3	19.2	15.4	17.9	-	-
	n	14	52	90	20	83	40	1	-	-