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

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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 Here we describe unpublished dentognathic material of ursids unearthed in the last field surveys performed at the cave, further comparing it with coeval chronologic and geographic sites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 sparse 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), Vallparadis 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 interfluvies 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 Villafranchian, 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. etruscus* 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, Ceysseguet 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 disatemas 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 lineage. 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 cusplids 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-kanivetzi* 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 an 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.

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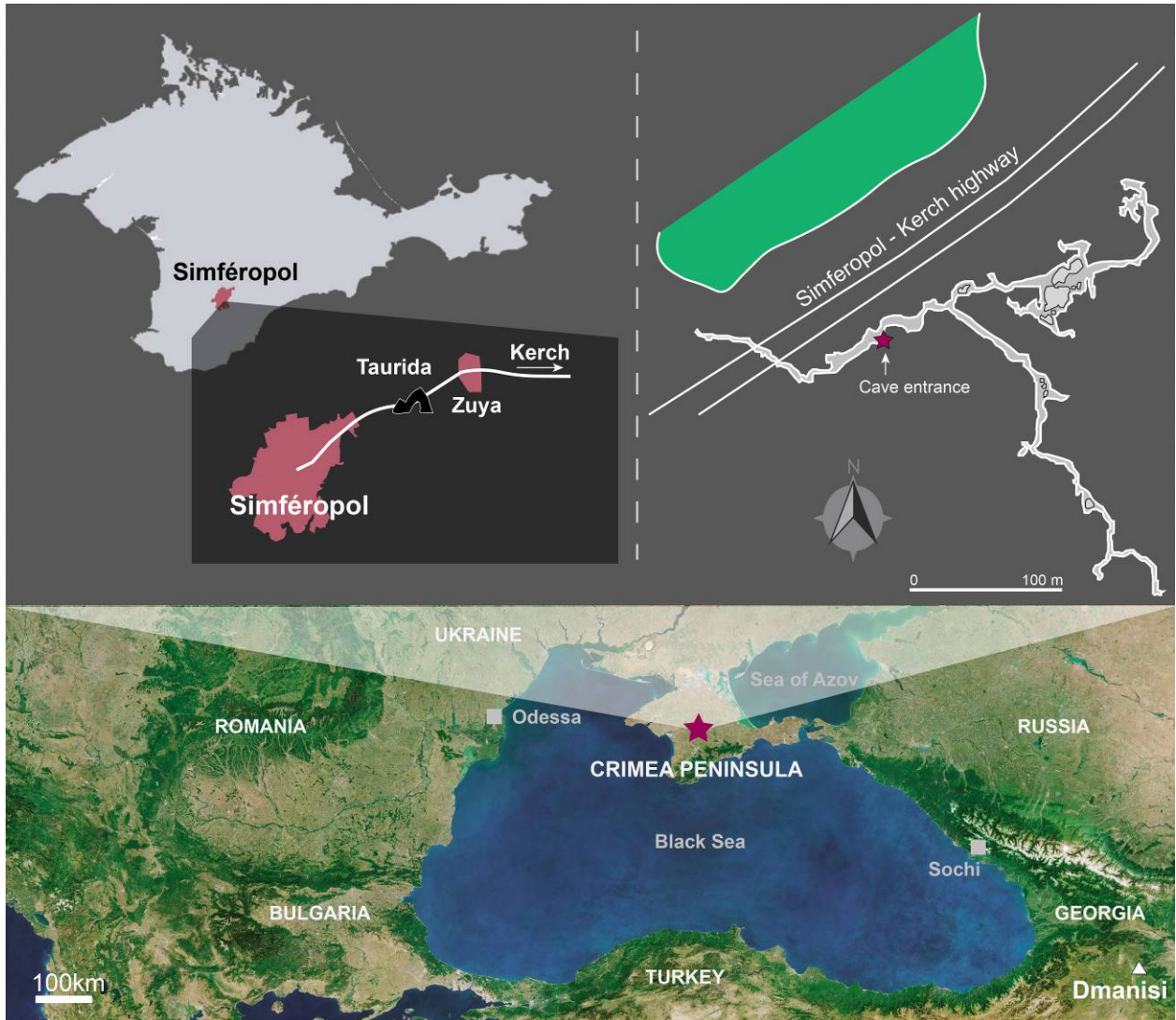
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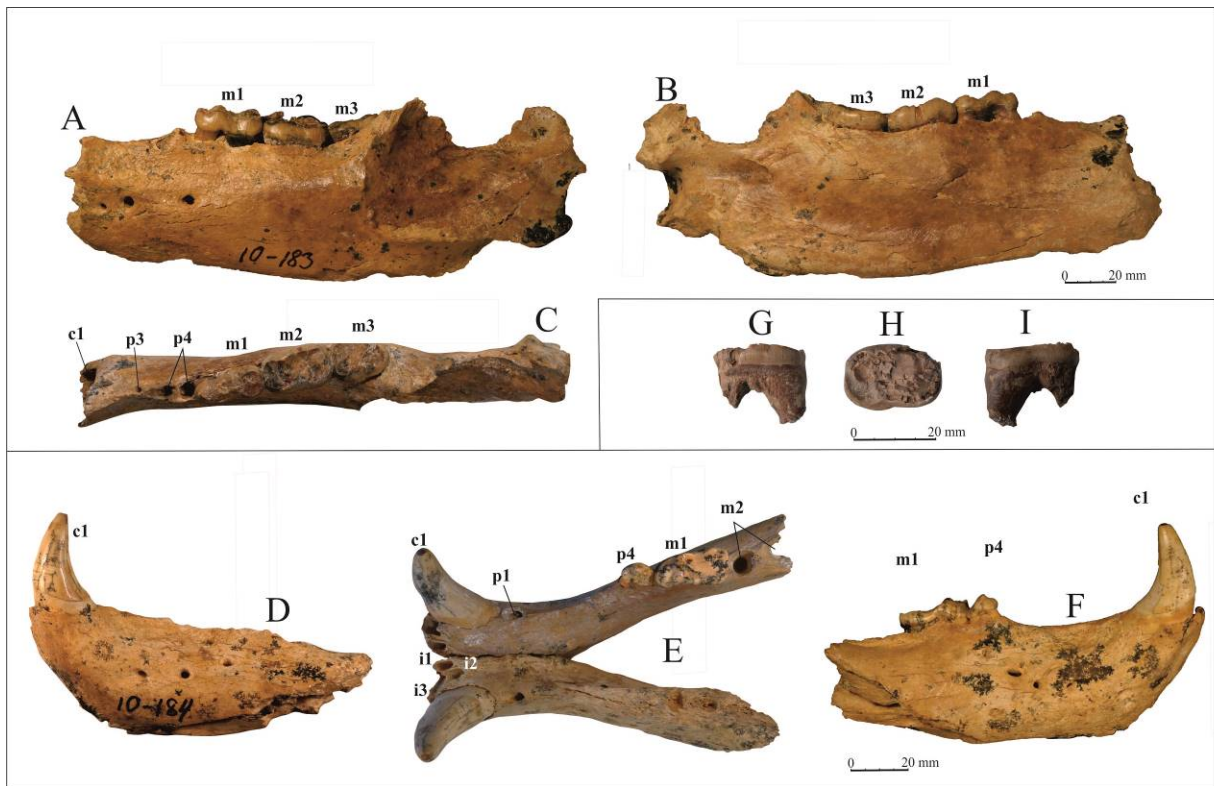
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### ***Figure captions***

**Figure 1.** Geographical location of the Taurida Cave within the Crimean peninsula and 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.

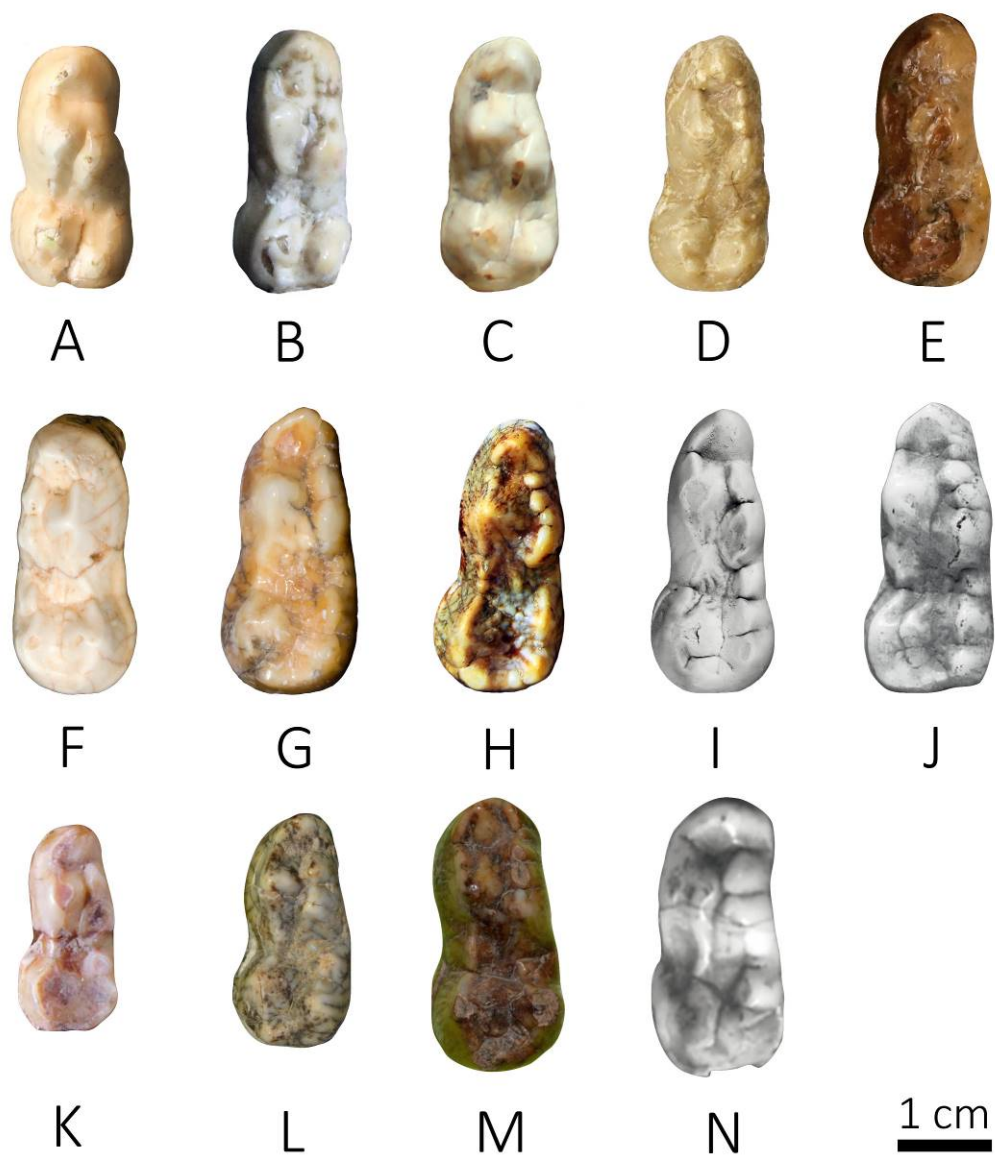


**Figure 3.** Corpora of Early Pleistocene *Ursus* species in buccal view. A-H *Ursus etruscus*: A Kuruksay (Russia, ca. 2.2. Ma) left corpus n° 3120-701; B Olivola (Italy, ca. 2.0 Ma) left corpus IGF4595; C Upper Valdarno (Italy, ca. 1.8Ma) left corpus IGF905; D Dmanisi (Georgia, ca. 1.8 Ma) left corpus 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.

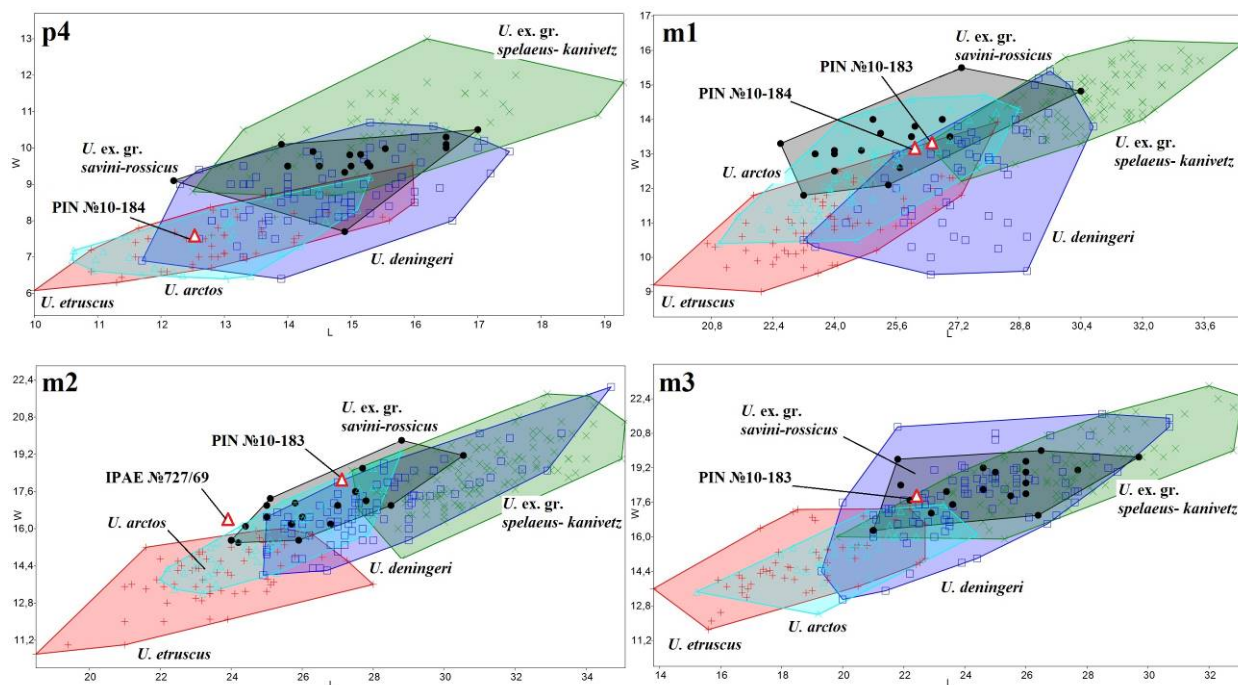


**Figure 4.** First lower molars of *U. etruscus* compared with of other Pleistocene members of the genus *Ursus* (occlusal view). A-E: *U. etruscus*, F-J: Cave bears, K-N: *U. arctos*. A Kuruksay left m1 n° 3120-701; B Olivola left m1 IGF4595; C Dmanisi left m1 D4940; D Venta Micena (Spain, ca.1.5 Ma) 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.



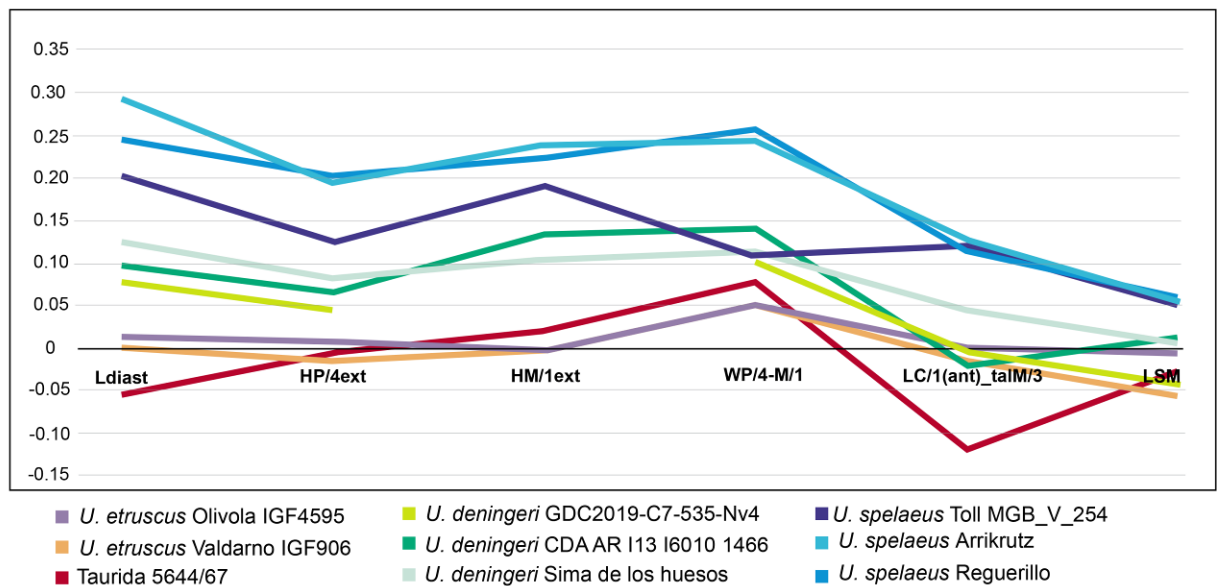
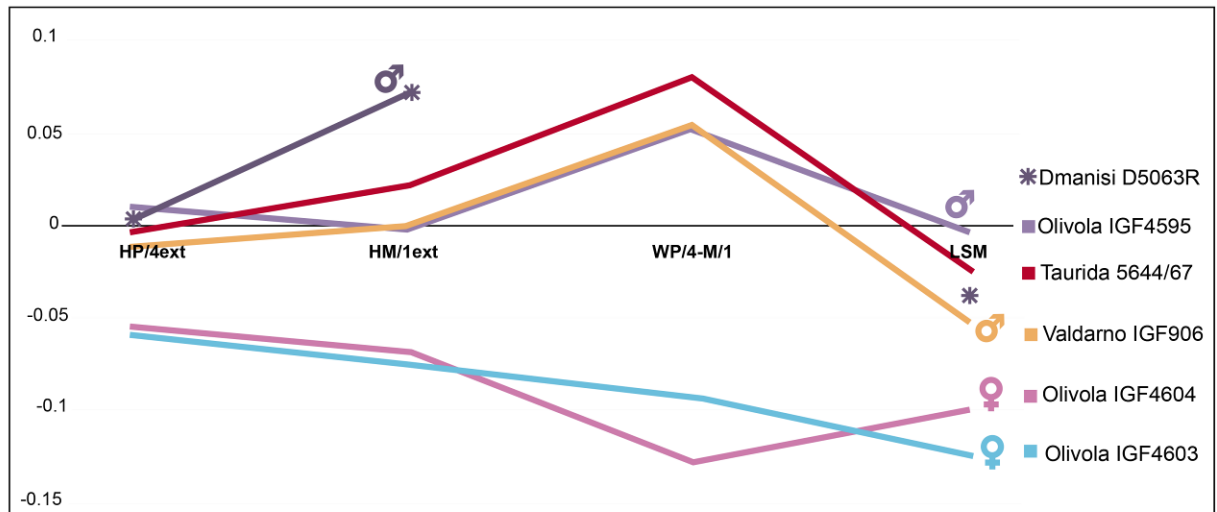
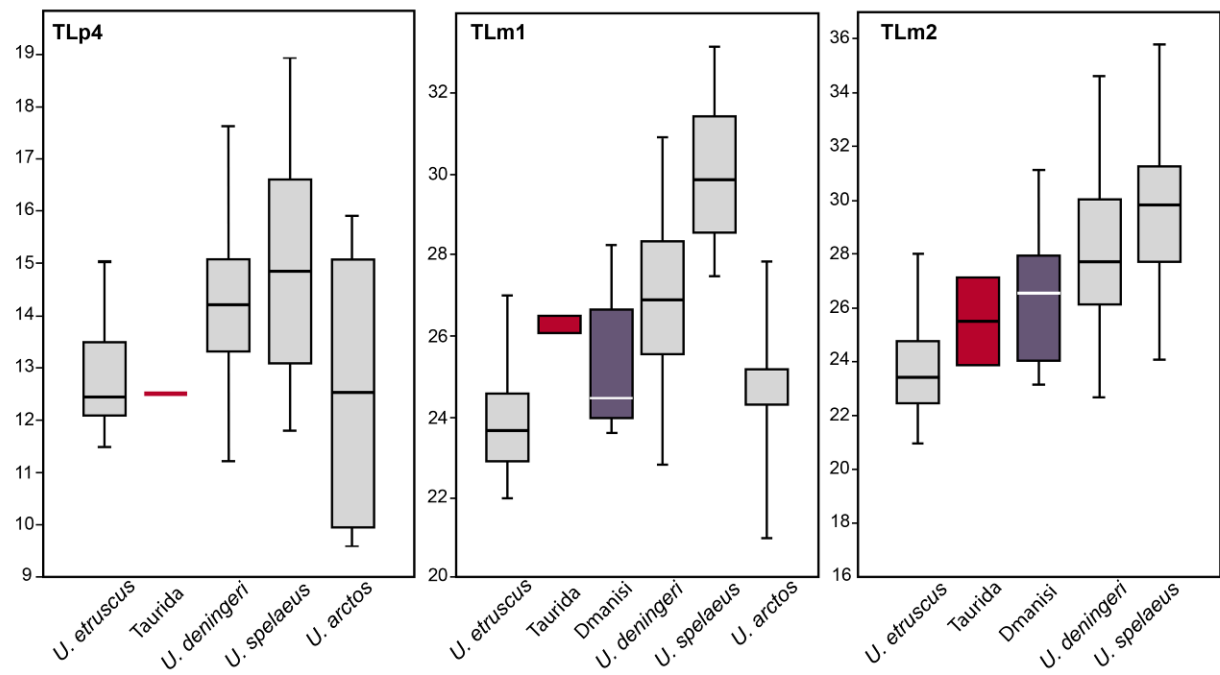


**Figure 5.** Biplots of mesidistal length versus buccolingual width of selected teeth of extant and fossil *Ursus* species.



**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 from coeval localities.





**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   |
|----------------------|---------------------------------|-----------------------------|--|
| <i>U. thibetanus</i> | 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;<br>Crégut-Bonnoure 1996;<br>Baryshnikov 2007 |
|                      | Gajtan                          | Albany                      | Fistani and Crégut-Bonnoure 1993   |
|                      | Achenheim                       | France                      | Dehm 1943;<br>Fistani and Crégut-Bonnoure 1993                                 |
|                      | Zhoukoudian 1                   | China                       | Pei 1934   |
| Imanay               | Russia                          | Gimranov 2019               |  |
| Šandalja I           | Croatia                         | Wagner et al. 2017          |  |
| <i>U. etruscus</i>   | 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                      | Mazza and Rustioni 1992;<br>Petrucchi et al. 2013                              |
|                      | Pirro Nord                      | Italy                       |  |
|                      | Saint-Vallier                   | France                      | Mazza and Rustioni 1992;<br>Baryshnikov 2007                                   |
|                      | Upper Valdarno                  | Italy                       |  |
|                      | Monte Argentario                | Italy                       | Petrucchi and Sardella 2009  |
|                      | Tsiotra Vryssi (TSR)            | Greece                      | Koufos et al. 2017   |
|                      | Tegelen, Netherlands            | Netherlands                 | Erdbrink 1953;<br>Viret,1954   |
|                      | Fuente Nueva-3                  | Spain                       | Medin et al. 2017  |
| Barranco León        |                                 |                             |  |
| Venta Micena         |                                 |                             |  |
| Dmanisi              | Georgia                         | Medin et al. 2019           |  |
| <i>U. deningeri</i>  | 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                   | France                      | Prat-Vericat et al. 2020   |
|                      | Grotte de la Carrière Sondage 1 |                             |  |
| Mosbach              | Germany                         | Soergel 1925;<br>Zapfe 1948 |  |

|                                     |                                 |             |                         |
|-------------------------------------|---------------------------------|-------------|-------------------------|
|                                     | Šandalja I                      | Croatia     | Wagner et al. 2017      |
|                                     | Vallonnet                       | France      | Moullé 1992             |
| <i>U. dolinensis</i>                | Atapuerca TD                    | Spain       | Garcia and Arsuaga 2001 |
| <i>U. deningeroides</i>             | Dripstone cave of Flatz         | Austria     | Rabeder et al. 2016     |
|                                     | Repolust                        | Austria     | Mottl 1964              |
| <i>U. ex. gr. savini-rossicus</i>   | Krasnodar                       | Russia      | Borissiak 1932          |
|                                     | Bachatsk                        |             | Baryshnikov 2007        |
|                                     | Berezhekovo                     |             |                         |
|                                     | Kudaro 1                        |             |                         |
|                                     | Mohovo                          |             |                         |
|                                     | Red Yar on the Ob River         |             |                         |
|                                     | Ulahan Sullar                   |             |                         |
|                                     | Mishin Kamik                    | Bulgaria    |                         |
| <i>U. ex. gr. spelaeus-kanivetz</i> | Steigelfadbalm                  | Switzerland | Frishauf 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                   |             |                         |
| <i>U. arctos</i>                    | A Valiña                        | Spain       | García 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 |             | <i>U. thibetanus</i> | <i>U. etruscus</i> | <i>U. deningeri</i> | <i>U. ex. gr. savini-rossicus</i> | <i>U. ex. gr. spelaeus-kanivetz</i> | <i>U. arctos</i> | <i>U. etruscus</i><br>PIN No. 5644/67 | <i>U. etruscus</i><br>PIN No. 5644/66 | <i>U. etruscus</i><br>IPAE No. 727/69 |
|-----------------|-------------|----------------------|--------------------|---------------------|-----------------------------------|-------------------------------------|------------------|---------------------------------------|---------------------------------------|---------------------------------------|
| <b>L p4</b>     | <b>Lim</b>  | 8.9-12.1             | 10.0-16.0          | 11.7-17.5           | 12.2-17.0                         | 12.5-19.3                           | 10.6-15.3        | -                                     | -                                     | -                                     |
|                 | <b>Mean</b> | 10.5                 | 13.0               | 14.6                | 15.1                              | 15.5                                | 12.9             | -                                     | 12.5                                  | -                                     |
|                 | <b>n</b>    | 11                   | 52                 | 79                  | 19                                | 57                                  | 35               | -                                     | 1                                     | -                                     |
| <b>W p4</b>     | <b>Lim</b>  | 5.8-7.7              | 6.1-9.5            | 6.4-10.7            | 7.7-10.5                          | 8.7-13.0                            | 6.4-9.2          | -                                     | -                                     | -                                     |
|                 | <b>Mean</b> | 6.4                  | 7.5                | 8.8                 | 9.6                               | 10.5                                | 7.5              | -                                     | 7.5                                   | -                                     |
|                 | <b>n</b>    | 11                   | 52                 | 79                  | 19                                | 57                                  | 35               | -                                     | 1                                     | -                                     |
| <b>L m1</b>     | <b>Lim</b>  | 18.8-22.3            | 19.3-28.2          | 23.2-30.7           | 22.6-30.4                         | 26.4-34.6                           | 21.0-28.8        | -                                     | -                                     | -                                     |
|                 | <b>Mean</b> | 20.6                 | 23.8               | 27.4                | 25.5                              | 30.6                                | 24.7             | 26.5                                  | 26.1                                  | -                                     |
|                 | <b>n</b>    | 13                   | 63                 | 56                  | 20                                | 93                                  | 68               | 1                                     | 1                                     | -                                     |
| <b>W m1</b>     | <b>Lim</b>  | 8.6-10.8             | 9.0-13.9           | 10.3-15.4           | 11.8-15.5                         | 12.2-16.3                           | 10.4-14.7        | -                                     | -                                     | -                                     |
|                 | <b>Mean</b> | 9.7                  | 11.0               | 12.7                | 13.4                              | 14.5                                | 12.4             | 13.3                                  | 13.2                                  | -                                     |
|                 | <b>n</b>    | 13                   | 63                 | 56                  | 20                                | 93                                  | 68               | 1                                     | 1                                     | -                                     |
| <b>L m2</b>     | <b>Lim</b>  | 19.3-23.1            | 18.5-28.0          | 24.9-34.7           | 24.0-30.5                         | 27.4-35.1                           | 22.0-28.8        | -                                     | -                                     | -                                     |
|                 | <b>Mean</b> | 21.0                 | 23.6               | 28.1                | 26.4                              | 31.1                                | 25.1             | 27.1                                  | -                                     | 23.9                                  |
|                 | <b>n</b>    | 12                   | 64                 | 84                  | 21                                | 115                                 | 52               | 1                                     | -                                     | 1                                     |
| <b>W m2</b>     | <b>Lim</b>  | 11.0-14.2            | 10.6-16.0          | 14.0-22.1           | 15.4-19.8                         | 14.7-21.8                           | 13.2-19.3        | -                                     | -                                     | -                                     |
|                 | <b>Mean</b> | 12.5                 | 14.0               | 16.9                | 17.0                              | 18.4                                | 15.6             | 18.1                                  | -                                     | 16.4                                  |
|                 | <b>n</b>    | 12                   | 64                 | 84                  | 21                                | 115                                 | 52               | 1                                     | -                                     | 1                                     |
| <b>L m3</b>     | <b>Lim</b>  | 14.2-19.2            | 13.8-22.7          | 19.3-30.7           | 21.0-29.7                         | 19.8-33.1                           | 15.2-24.4        | -                                     | -                                     | -                                     |
|                 | <b>Mean</b> | 16.2                 | 18.7               | 24.4                | 24.8                              | 27.4                                | 20.4             | 22.4                                  | -                                     | -                                     |
|                 | <b>n</b>    | 14                   | 52                 | 90                  | 20                                | 83                                  | 40               | 1                                     | -                                     | -                                     |
| <b>W m3</b>     | <b>Lim</b>  | 8.9-14.8             | 11.7-17.3          | 13.1-21.7           | 16.3-20.0                         | 15.9-23.0                           | 12.4-17.5        | -                                     | -                                     | -                                     |
|                 | <b>Mean</b> | 12.1                 | 14.7               | 17.8                | 18.3                              | 19.2                                | 15.4             | 17.9                                  | -                                     | -                                     |
|                 | <b>n</b>    | 14                   | 52                 | 90                  | 20                                | 83                                  | 40               | 1                                     | -                                     | -                                     |