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# *Ursus etruscus* from the late Early Pleistocene of the Taurida cave (Crimean Peninsula)

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**ABSTRACT**

The present work describes the dentognathic remains of *Ursus etruscus* Cuvier, 1823 from the recently discovered Taurida cave in central Crimea at the north Black Sea area. The bone-bearing layer of Taurida cave corresponds to the Psekupsian Faunal Assemblage of Eastern Europe and to the Late Villafranchian of Western Europe (ca. 1.8–1.5 Ma). Here, we describe unpublished ursid material unearthed during the excavations performed at the cave in 2020–2021, further comparing it with coeval chronologic and geographic sites around Europe. Our anatomical and biometrical analyses suggest 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 provide a link between the western and eastern parts of the species range. Therefore, the finds from Crimea are important for understanding of the morphological diversity and evolution of *U. etruscus* which is the putative ancestor of both cave bears and brown bears. Furthermore, the study of these remains is also important for understanding the processes of the forming of the large mammal assemblages in the late Early Pleistocene and its relationships with the dispersal of the genus *Homo*.

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**KEYWORDS**
*Ursus etruscus*; *U. arctos*; cave bears; Early Pleistocene; Crimean Peninsula; Taurida cave

## Introduction

*Ursus etruscus* Cuvier, 1823, is 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-Pairó 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 scarce finds at East and Central Asia and North Africa are also noteworthy, evidencing a wide geographical range during the Early Pleistocene (Baryshnikov 2007; Jiangzuo et al. 2018). Throughout this chronologically long record, two main different morphotypes of *U. etruscus* can be distinguished: an early form from the Middle Villafranchian (e.g., Saint-Vallier or Kuruksay) and late form 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* von Reichenau, 1904) were recorded in Europe at sites such as Le Vallonnet (1.2 Ma; France; Moullé 1992), Vallparadís Section (1.0–0.8 Ma; Spain; Madurell-Malapeira et al. 2010, 2014) or Untermassfeld (= *Ursus rodei* Musil, 2001; 1.0 Ma; Germany; Musil 2001).

In turn, the first European record of the brown bear (arctoid) lineage (*U. arctos* Linnaeus, 1758), 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 Čermák 2012). Several authors consider the latest Early Pleistocene European forms putatively related with the brown bear lineage including the remains from Deutch-Altenburg, Untermassfeld or Gran Dolina TD6 (Rabeder et al. 2010; Wagner and Čermák 2012; see a review in Madurell-Malapeira et al., 2021). However, the first undisputed brown bear record in Western Europe comes 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 analysed 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 the Taurida cave

Taurida cave was discovered in Crimea in 2018, being located 15 km east of Simferopol (45°02′37′′N, 34°17′09′′E) at the Crimean Peninsula (Figure 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 deposits of the Paleogene nummulite limestones (Simferopol Stage).

The preliminary analysis of the fossil vertebrate remains from Taurida cave suggested the Late Villafranchian age for the bone-bearing deposits (Lopatin 2019a, 2019b; Lopatin et al. 2019; Zelenkov et al. 2019; Gimranov et al. 2020, 2021; Lavrov et al. 2020, 2021a, 2021b, 2021c; Oksinenko and Lavrov 2021). Throughout the Late Villafranchian, the cave was connected to

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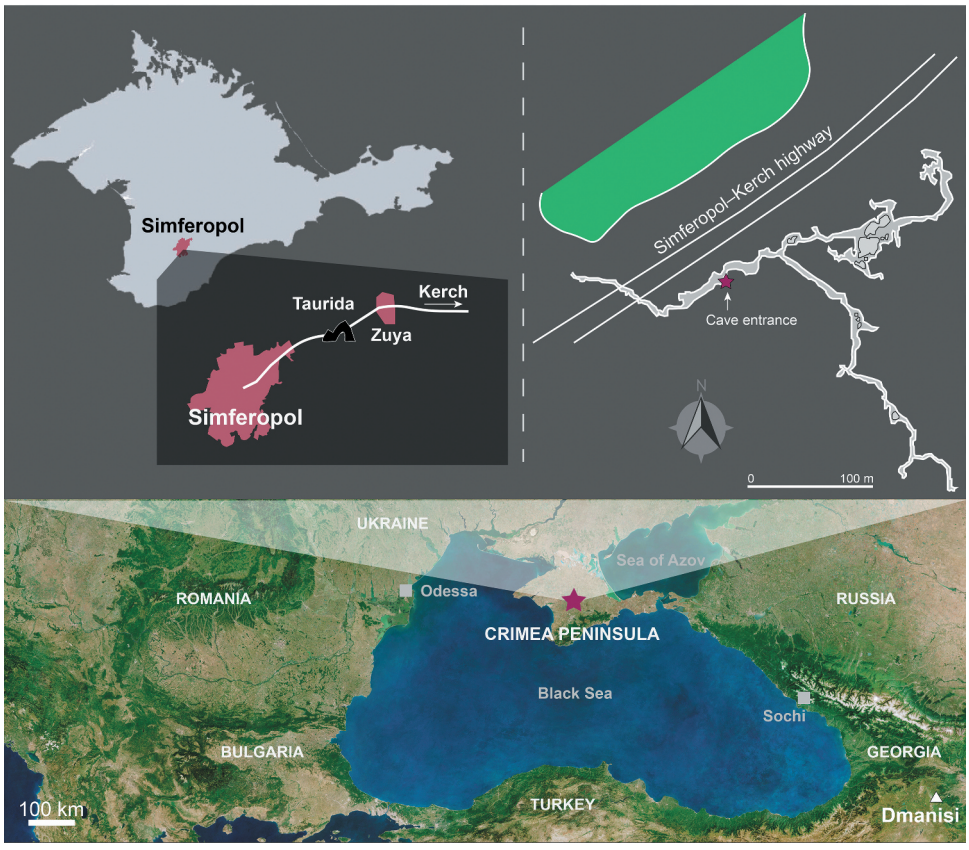


**Figure 1.** Geographical position of the Taurida cave within the Crimean Peninsula and topography of the cave (modified from Zelenkov et al. 2019).

the day surface through a wide (2–3 m wide and about 2–3 m high) horizontal southern corridor, opened on the slope of the left side of the ancient Fundukla valley (Oksinenko and Lavrov 2021).

The remains of fossil bears were found by the first two authors in the near-surface layer of deposits in a small cave chamber called the 'Hyena Den'. The bone-bearing layer of the cave is represented by red-brown loams of subaerial genesis. The faunal list includes the following species: birds *Pachystruthio dmanisensis, Tetrao* sp., *Accipiter* cf. *gentilis*, Falconidae gen. indet., mammals *Erinaceus* sp., *Crocidura kornfeldi, Beremendia fissidens, Hypolagus brachygnathus, Lepus* sp., *Spermophilus nogaici, Hystrix* (*Acanthion*) *vinogradovi, H. (H.) refossa, Sicista* sp., *Apodemus* sp., *Allocricetus ehiki, Cricetus* sp., *Clethrionomys* sp., *Ellobius kujalnikensis, Lagurodon arankae, Mimomys* sp., *Allophaiomys deucalion, Canis* sp., *Vulpes alopecoides, Ursus etruscus, Pachycrocuta brevirostris, Homotherium crenatidens, Megantereon adroveri, Lynx issiodorensis, Archidiskodon meridionalis, Equus* sp., *Elasmotherium* sp., *Stephanorhinus* sp., *Paracamelus gigas, Arvernoceros verestchagini, Leptobos* sp., *Bison* (*Eobison*) sp., *Gazellospira torticornis*, and *Pontoceros ambiguus* (Lopatin et al. 2019; Zelenkov et al. 2019; Gimranov et al. 2020, 2021; Lavrov et al. 2021b; Lopatin 2021; Lopatin and Tesakov 2021). The co-occurrence of representatives of *Leptobos* sp. and *Bison* (*Eobison*) sp. makes it possible to determine the age of the deposits from 1.8 to 1.5 Ma (Lopatin et al. 2019; Vislobokova et al. 2020a, 2020b). Analysis of the species composition of the Taurida cave indicates its correspondence to the Psekupsian Faunal Assemblage of Eastern Europe, which corresponds to the Late Villafranchian, the Mammalian Zone MNQ18. The revised Quaternary time scale of Gibbard et al. (2010) for chronological references is used in this article.

Concerning the ursids of Taurida cave, previously we described a fragment of the facial part of the Etruscan bear skull (specimen PIN no. 5644/65) from the 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 diastemata, 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) gave the reason 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 the Taurida locality and other Pleistocene samples from Europe. Two hemimandibles from Taurida cave are housed at the PIN (Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow) and one tooth is housed at the IPAE (Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg). The comparative fossil material from the Middle–Late Villafranchian and Epivillafranchian of 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 following localities: 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. (2018).

*Dental anatomical abbreviations* – lower premolars: p1, p2, p3, p4; lower molars: m1, m2, m3.

*Measurement abbreviations* – H, height; L, length; W, width.

*Institutional abbreviations* – D: catalogue number of the Dmanisi collections of the S. Janashia Museum of Georgia, Georgian National Museum (Tbilisi, Georgia); ICP: Institut Català de Paleontologia Miquel Crusafont (Sabadell, Spain); IGF: Natural History Museum, Geology and Palaeontology Section, University of Florence (Italy); IPAE: Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences (Yekaterinburg, Russia); MAEG: Museo Arqueológico y Etnológico (Granada, Spain); MPRM: Musée de Préhistoire Régionale (Menton, France); PIN: Borissiak Paleontological Institute, Russian Academy of Sciences (Moscow, Russia).

Due to the fact that researchers do not have an unambiguous opinion on Latin name for the small cave bear *Ursus savini* Andrew, 1922 or *U. rossicus* Borissiak, 1930 (Baryshnikov 2007; Rabeder et al. 2010; Wagner and Čermák 2012; Baryshnikov and 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 separated (Hofreiter et al. 2007; Krause et al. 2008; Knapp et al. 2009; Stiller et al. 2014; Barlow et al. 2016, 2018, 2019, 2020). By the reason that not all cave bears from the Late Pleistocene have been genetically studied, we suppose that it is possible to consider them as *U.* ex. gr. *spelaeus–kanivetz*.

**Table 1.** Measurements of *Ursus 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 | - | - |

* alveolus is broken, ** measurements along the right ramus of the mandible

## *Systematic palaeontology*

## Order Carnivora Bowdich, 1821

## Family Ursidae Fischer de Waldheim, 1814

## Subfamily Ursinae Fischer de Waldheim, 1814

## Genus *Ursus* Linnaeus, 1758

## *Ursus etruscus* Cuvier, 1823

## *Figures 2–4*

### *Referred specimens*

Partial left mandibular ramus with m1–m3 (PIN no. 5644/67; Figure 2(a–c)); incomplete right and left mandibular corpora with both c1 and p4–m1 (PIN no. 5644/66; Figure 2(d–f)); right m2 (IPAE no. 727/69; Figure 2(g–i)).

### *Measurements*

Table 1.

## Description

*Corpus* – The specimen PIN no. 5644/67 preserve the left corpus. The corpus is high and has a medium degree of robusticity. The specimen belongs to an old individual: m1–m3 are quite worn. The overall size of the corpus is similar to a large extant *U. arctos*. The anterior margin of the masseteric 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 mandibular foramen. There are four mental foramina, located below diastema of c1–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, only 19.8 mm long.

In the specimen PIN no. 5644/66, the incisors are absent in both corpora. Both c1 are preserved. Alveoli of p1, p4, and m1, and the incomplete alveolus of m2 are present in the right corpus. The left corpus was broken at the level of the anterior part of the m2 alveolus. There are five mental foramina on the right corpus and four in the left one. The corpora are slender, with long diastemata (Figure 2(d–f)).

*Dentition* – The p4 is absent in the specimen PIN no. 5644/67, but its alveoli are 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 worn 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. 2018) arises towards the centre of the hypoconid. There are no additional structures between metaconid and entoconid. The entoconid complex consists of one cusp. The buccal cingulid 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 an entoconid complex consists of two

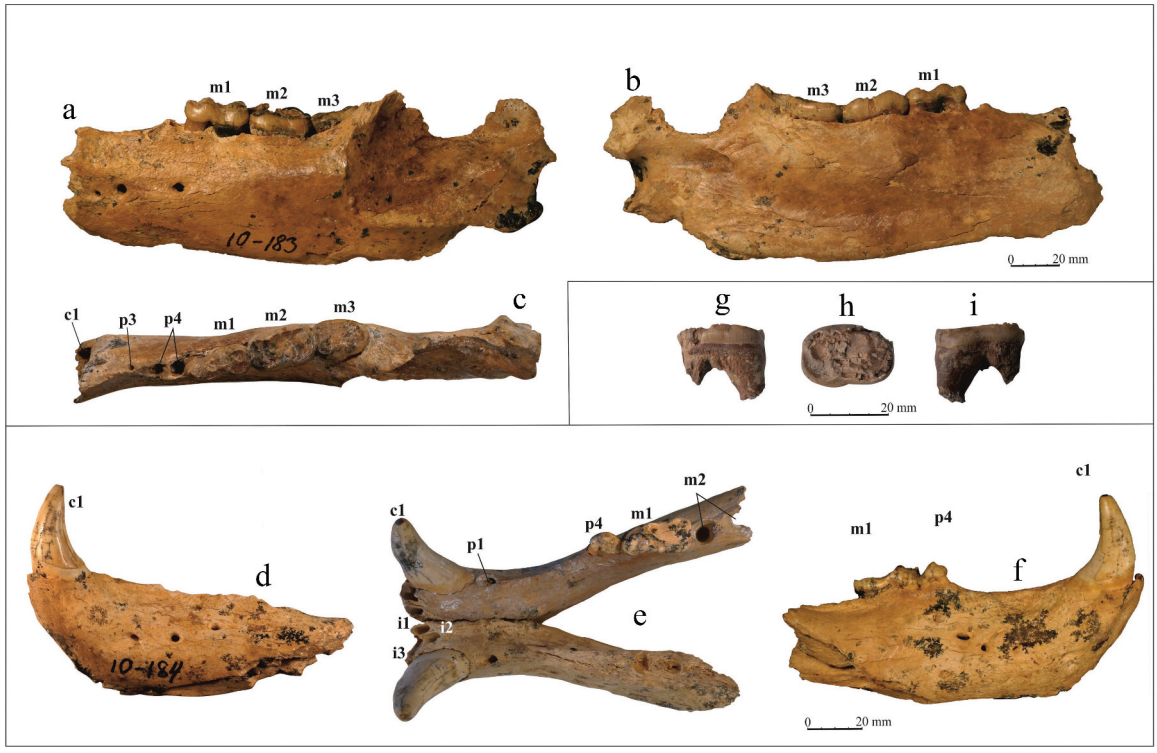


**Figure 2.** Dentognathic specimens of *Ursus etruscus* from the Taurida cave. Specimen PIN no. 5644/67, fragment of left corpus with m1–m3 in (a) buccal, (b) lingual, and (c) occlusal views. Specimen PIN no. 5644/66, left and right partial corpora with right p4–m1 in (d) left buccal, (e) occlusal, and (f) right buccal views. Specimen IPAE no. 727/69, right m2 in (g) buccal, (h) occlusal, and (i) lingual views.

cusps (entoconid 1 and entoconid 2) which are approximately equal to each other in size. The m3 is oval shaped, without a hypoflexid. The metaconid is ridge-like and small.

The both mandibular rami in the specimen PIN no. 5644/66 display relatively large p1 alveoli. The alveoli of p2 and p3 are absent. The right p4 is oval shaped, has no additional cusps except for a tiny cusp on the distal cristid of the protoconid. In addition, there is a rudimentary mesial cusp which appears as a basal thickening of the main cone. The m1 displays the apex of the protoconid poorly distinguishable, the buccal margin of the protoconid is strongly worn out, and the preserved lingual margin 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 and narrower than the talonid. 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 IPAE no. 727/69 (Figure 2(g–i)) is oval in shape, has a slightly pronounced hypoflexid. The talonid is elongate relative to the trigonid and takes up 36.4% of the total length of the tooth. The trigonid of 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 cingulid on the buccal side at the point of contact between the trigonid and talonid.

## Discussion

### *Morphological comparisons of the Taurida bear 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 and comparing it with the known Early Pleistocene European representatives.

The studied specimens display high and robust corpora (Figure 2(a,d)). The pterygoid process, an attachment surface of the pterygoid muscle (*m. pterygoideus medialis pars anterior*), situated approximately below mandibular foramen, is very prominent. This structure is typical for the arctoid forms according to García and Arsuaga (2001) and Madurell-Malapeira et al. (2010).

Concerning anterior premolars (p1–p3), the studied specimens show alveoli of p1, p2 and p3 (Figure 2(c,e); Figure 3). In the early forms of *U. etruscus* (Saint-Vallier, Kuruksay) all premolars are present and closely attached to each other (Figure 3), meanwhile in the advanced forms (Dmanisi, Pietrafitta) the diastemata appears between p1–p2 and p2–p3. Later, in Epivillafranchian forms of *U. deningeri* (Vallonnet or Cal Guardiola), these anterior premolars are present sometimes only, always lacking p2 (Figure 3; J. M.-M. pers. observ.). As clearly visible in Figure 3, the Taurida specimens display a distribution and composition of anterior premolars similar to Dmanisi or Pietrafitta.

The p4 of the specimen PIN no. 5644/66 displays an oval shape in occlusal view, with no additional cusps, except for a tiny cusp on the posterior cristid of the 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 speleoid lineage. The p4 of cave bears are characterised by the presence of additional cusps on the posterior protoconid cristid (postprotocristid), with anterior and posterior additional cusps (Rabeder 1999; Baryshnikov 2007; Wagner and Čermák 2012; Prat-Vericat et al. 2020). The Pleistocene *U. arctos* is characterised by p4 with anterior and posterior additional cusps (Gimranov 2018). Extant *U. arctos*


**Figure 3.** Corpora of Early Pleistocene *Ursus* species in occlusal view. a–h, *Ursus etruscus*: (a) Kuruksay (Tajikistan, ca. 2.2. Ma), left corpus, PIN no. 3120/701; (b) Olivola (Italy, ca. 2.0 Ma), left corpus, IGF4595; (c) Upper Valdarno (Italy, ca. 1.8 Ma), 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.

is characterised by p4 without additional cusps on the posterior protoconid cristid (morphotype A2, occurrence 23.8%) or by p4 with these cusps (morphotype A3, occurrence 36.3%). Note that the early evolutionary stage of the Etruscan bear (Saint-Vallier and Kuruksay localities) is characterised 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 characterised by a simpler p4 structure, without additional cusps (Mazza and Rustioni 1992; Medin et al. 2019).

The m1 displays 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 (Figure 4(a–e)) are characteristic of *U. etruscus* (Mazza and Rustioni 1992; Baryshnikov 2007) and distinguish it from brown and speleoid bears (Figure 4(f–n)). Fossil and extant *U. arctos* are characterised by m1 (Figure 4(k–n)) with a bicuspid or tricuspid metaconid and bicuspid entoconid (Baryshnikov 2007; Wagner and Čermák 2012). The m1 of speleoid bears (Figure 4(f–j)) are characterised 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 (Rabeder 1999; Baryshnikov 2007; Wagner and Čermák 2012; Prat-Vericat et al. 2020). The metaconid complex of m1 consists of a single cusp in the specimen PIN no. 5644/67 and brings it closer to *U. etruscus* from Saint-Vallier and Kuruksay, which belong to the early evolutionary stage of the Etruscan bears (Mazza and Rustioni 1992; Baryshnikov 2007).

The m2 of the specimen PIN no. 5644/67 has bicuspid entoconid with approximately equal cusp size. A similar structure is typical for *U. etruscus, U. arctos* and speleoid bears (Mazza and Rustioni 1992; Rabeder 1999; Baryshnikov 2007; Wagner and Čermák 2012; Prat-Vericat et al. 2020). The m2 talonid of the specimen 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 (Saint-Vallier and Kuruksay). The Etruscan bears of the late evolutionary stage (Upper Valdarno, Olivola, Pietrafitta or Dmanisi) are characterised by the mesiodistally elongated talonid of m2 (Baryshnikov 2007).

The m3 of the specimen 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 included here in the hypodigm of *U. etruscus* on the basis of the following features: presence of p1, p2 and p3; short diastema between c1–p4; p4 with oval shape and without additional cusps; and metaconid and entoconid complexes of m1 containing one cusp each and demonstrating the absence of additional elements (cusps and cristids) between the metaconid and entoconid. A number of other features, such as a robust corpus, m1 unicuspid metaconid, and a moderately short talonid of m2, also indicates the similarity of *U. etruscus* (PIN no. 5644/67) from Crimea with the subspecies *U. e. verescagini* Sharapov, 1986 and *U. e. saintvallierensis* Baryshnikov, 2007, which are the early evolutionary stage of Etruscan bears (Baryshnikov 2007).

## Biometrical comparisons of the Taurida bear with coeval European finds

Taking into account the fragmentary nature of the studied specimens we performed biplot (Figure 5), boxplots and log ratio diagrams (Figure 6) of selected dental elements comparing the Taurida specimens with fossil and extant ursids (data collected from various publications, see Table 2, and unpublished data from the 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 display the largest dimensions on all the analysed variables. On the four analysed variables of Figure 5 (p4, m1, m2 and m3) *U. etruscus* and Pleistocene *U. arctos* display 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*

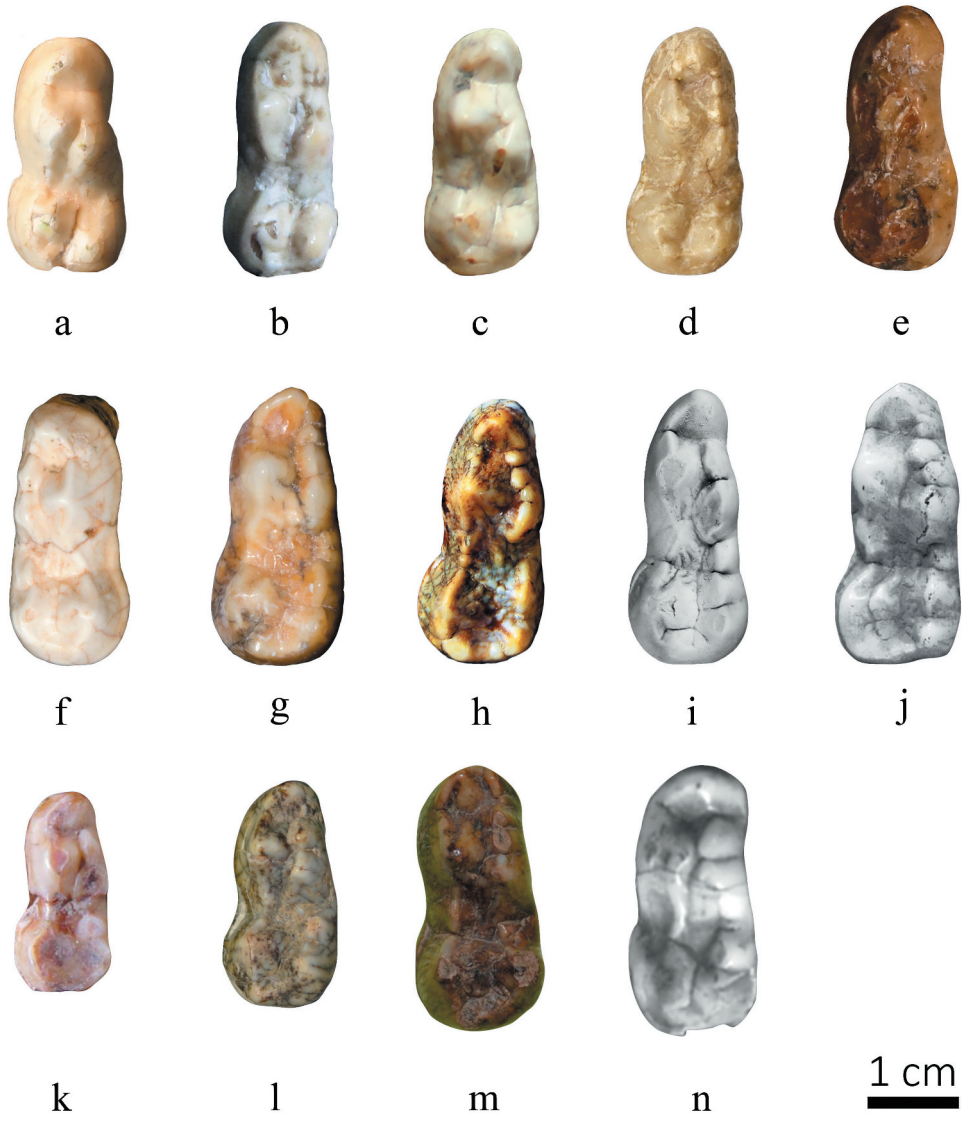


**Figure 4.** First lower molars of *U. etruscus* compared with those of other Pleistocene members of the genus *Ursus* (occlusal views). a–e: *U. etruscus*; f–j: cave bears; k–n: *U. arctos*. (a) Kuruksay, left m1, PIN no. 3120/701; (b) Olivola, left m1, IGF4595; (c) Dmanisi, left m1, D4940; (d) Venta Micena (Spain, ca.1.5 Ma), right m1, VM10318; (e) Taurida cave, PIN no. 5644/67; (f) Vallonnet (*U. deningeri*, France, ca. 1.2 Ma), 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 (Russia), right m1, IPAE no. 802/1338; (m) Severnaya Cave (Russia), left m1, IPAE no. 2079/241; and (n) Zoolithenhöhle (Germany), left m1, NHM O.C.1.

and *U. deningeri* occupy an intermediate position between large-sized and small-sized samples. In general, the clouds of distribution of all samples strongly overlap.

*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 the specimen PIN no. 5644/66 falls into the centre 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 Figure 6 show 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 the Taurida cave (PIN nos. 5644/66 and 5644/67) 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 centre 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 Figure 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 bears (PIN no. 5644/67; IPAE no. 727/69) 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 displays a wide range of variability for Taurida specimens: the specimen PIN no. 5644/67 falls near the centre distribution for *U.* ex. gr. *savini–rossicus*; the specimen IPAE no. 727/69 close the values for *U. etruscus* and *U. arctos* and finally the specimen IPAE no. 727/69 closer to the areas of distribution of *U. etruscus*, *U.* ex. gr. *savini–rossicus* and *U. arctos*. Finally, Figure 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*.

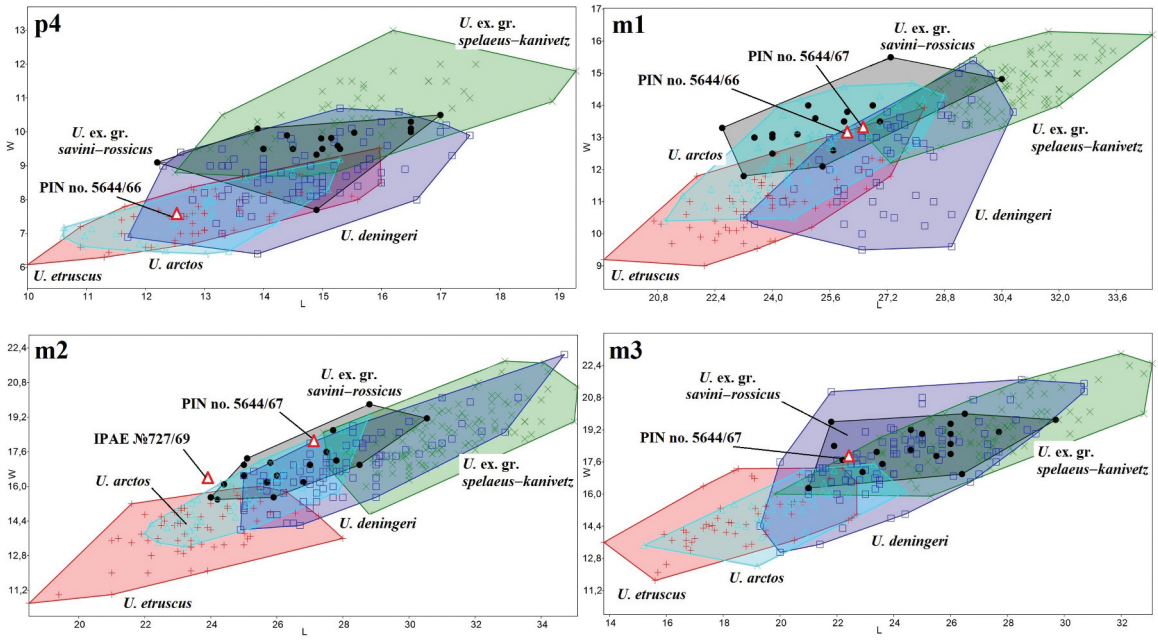


**Figure 5.** Biplots of mesiodistal length (L) versus buccolingual width (W) of selected teeth of extant and fossil *Ursus* species.

*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 displays the former specimen located close to the centre 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 Figure 6, which also analyse corpus variables as longitude of the diastema, show in the first time that the Taurida specimens follow a similar pattern as compared with Dmanisi, Olivola and Upper Valdarno male specimens and in the 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 (Figure 6).

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

## Comments on the interrelationships between the Etruscan bear and the members of the Taurida faunal assemblage

*U. etruscus* co-existed with a variety of highly specialised large carnivorans, such as lynx (*Lynx issiodorensis)*, giant hyenas (*Pachycrocuta brevirostris*) and sabre-toothed cats (*Homotherium crenatidens* and *Megantereon adroveri*). Also, the Etruscan bear had to compete with members of the genus *Canis*, the remains of which, along with felines and hyenas, were found in the Taurida cave (Gimranov et al. 2020; Lavrov et al. 2020, 2021b).

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* and *Homotherium* 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 relationships of the carnivore guild from this locality with the dispersal of the early *Homo*. This was previously stated when the finds of *Pachystruthio* in the Taurida cave being described (Zelenkov et al. 2019). It is also noteworthy to highlight the faunal similarities between the Taurida and Dmanisi sites, from where the earliest Eurasian remains of *Homo* are known (Lordkipanidze et al. 2013). In fact, as recently stated by Bartolini-Lucenti and colleagues (2022), the Dmanisi carnivore guild is the most similar to the European assemblages from the Late Villafranchian, such as Venta Micena or Pirro Nord, than to African or Asian ones. Unfortunately, the Taurida carnivore guild was not included in the former study; however, the Late Villafranchian character of the Taurida cave is undoubtable, sharing with Dmanisi practically all the large carnivores, i.e., *Homotherium, Megantereon, Pachycrocuta, U. etruscus* and *Canis*. Incomplete identity of the Dmanisi and Taurida guilds is a matter of sampling because the latter site was recently discovered.

Another important fact should be noted. There are no 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 (so-called 'suid gap') with aridization 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 faunal assemblages of Dmanisi and Taurida cave brings these two localities together and makes a closer connection of Taurida fauna with the early *Homo* dispersal in Europe.

The finds of *U. etruscus* from Taurida cave described above probably marks the southernmost distribution area for this species in Eastern Europe. The Crimean Peninsula is located at the junction

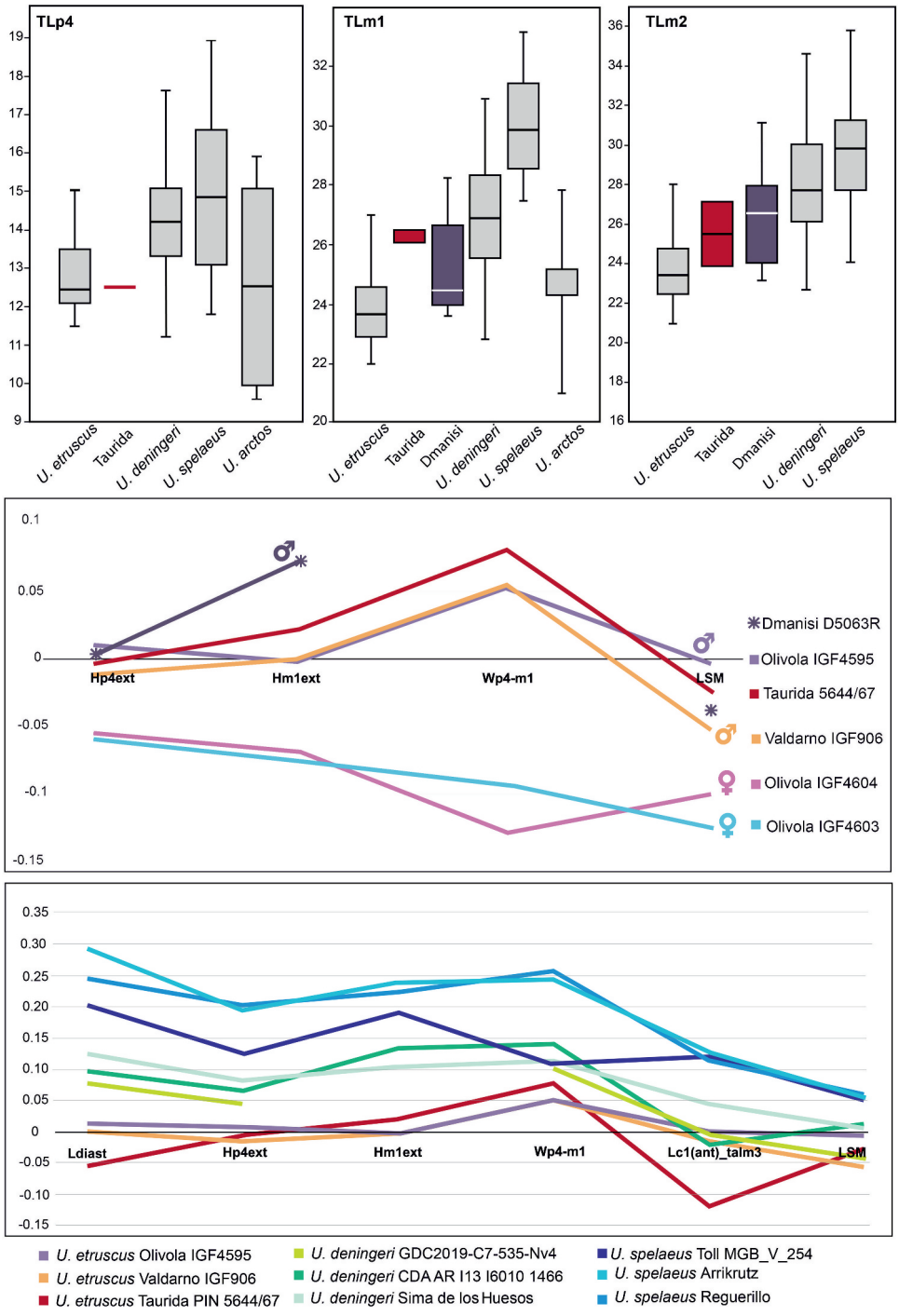


**Figure 6.** Boxplots of selected dental elements on Pleistocene and extant *Ursus* species on the top and log ratios of dentognathic variables comparing the Taurida sample with fossil bear specimens form coeval localities. Abbreviations: TLp4, p4 total length; TLm1, m1 total length; TLm2, m2 total length; Hp4ext, mandibular height at the p4 measured buccally; Hm1ext, mandibular height at the m1 measured buccally; Wp4-m1, mandibular width at the p4-m1; Lc1(ant)-talm3, mandibular length measured between the anterior edge of c1 and distal m3.

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.

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

| Species | Locality | Country | Published data |
|---|---|---|---|
| *U. thibetanus* | Azykh | Azerbaijan | Baryshnikov 2007 |
| | Mauer | Germany | |
| | Miyata | Japan | |
| | Perpignan | France | |
| | Kudaro 1 | South Ossetia | 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 |

(*Continued*)

**Table 2.** (Continued).

| Species | Locality | Country | Published data |
|---|---|---|---|
| *U. deningeri* | Bilzingsleben | Czech Republic | Musil 1991; Musil 2005 |
| | Stránská skála | Czech Republic | Musil 1972 |
| | Caune de l'Arago | France | Quilès 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 | García 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 | | |
| | Mohovo | | |
| | Red Yaron the Ob River | | |
| | Ulahan Sullar | | Boeskorov et al. 2012 |
| | Kudaro 1 | South Ossetia | Baryshnikov 2007 |
| | Mishin Kamik | Bulgaria | Spassov et al. 2017 |
| *U.* ex. gr. *spelaeus – kanivetz* | Steigelfadbalm | Switzerland | Frischauf et al. 2017 |
| | Arbreda | Spain | Quilès 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 | | |

(*Continued*)

**Table 2.** (Continued).

| Species | Locality | Country | Published data |
|---|---|---|---|
| *U. arctos* | 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 | Quilès 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 Chukochya River | Russia | Boeskorov and Baryshnikov 2013 |
| | Kyra-Sullar | | |
| | Mamontova Gora | | |
| | Oshbordoh | | |
| | Kudaro 3 | South Ossetia | Baryshnikov 2010 |
| | Eliseevichi | Russia | |
| | Aman-Kutan | Uzbekistan | |
| | Genista Cave | Gibraltar | |
| | Koneprusy | Czech Republic | |
| | Predmosti | | |
| | Monte Verde | Italy | |
| | Taubach | Germany | |
| | Chatillon-Saint-Jeans | France | Baryshnikov 2007 |
| | Ingarano | Italy | |
| | Zoolithenhöhle | Germany | Pacher, 2007 |

**Table 3.** Length (L) and width (W) of teeth of the Ursidae inhabiting the territory of Eurasia in the 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 | - | - |

## Conclusions

Dentognathic remains of a medium-sized ursid from Taurida cave in Crimea are described. The morphological variability observed in the studied specimens enabled us to include it in a late 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. 1.8 Ma) 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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