

Etruscan Wolf *Canis etruscus* (Canidae, Carnivora) from the Early Pleistocene of Crimea (Taurida Cave)

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Abstract—The cranial and mandibular fragments of the medium-sized canid from the Early Pleistocene locality of Taurida cave (about 1.8–1.5 Ma) in Crimea are described and included in the hypodigm of the species *Canis etruscus* Forsyth Major, 1877, a common member of the Late Villafranchian fauna of the Circum-Mediterranean region. This species is reported for the first time from the Northern Black Sea region. The discovered evidence reinforce previous published idea regarding the periodically use of the Taurida cave by canids and other large predators as a den and shelter.

Keywords: *Canis etruscus*, Early Pleistocene, Taurida cave, Crimea, premolars, molars, evolution

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Numerous remains of Carnivora were found in the Taurida cave, including Canidae, Ursidae, Felidae, Hyaenidae, and Mustelidae [1–4]. All finds correspond to the Late Villafranchian Faunal Unit of Western Europe (Psekupsian Faunal Assemblage of southern Russia, approximately 1.8–1.5 Ma) [1]. The studied canid remains were discovered in the southern corridor of the cave, at a distance of up to 200 m from the ancient natural entrance to cave (it was on the slope of the Fundukla River valley). Through this horizontal corridor, ancient predators entered the cave, which they used as a den. The bones of ungulates found in the cave are the product of the hunting of these animals [5].

Within the unearthed canid remains, the most common specimens correspond to a medium-sized wolf, which is overall smaller than the extant *Canis lupus* Linnaeus, 1758. The first dispersal of the genus *Canis* Linnaeus, 1758 in Western Europe has long been considered a biochronological marker of the beginning of the Late Villafranchian (ca. 2.0 Ma) and was informally called a “Wolf-Event” [6–8]. Subsequently, it was shown that the first appearance of the genus *Canis* in Europe took place in the Middle Villa-

franchian, in the faunal unit of the Costa San Giacomo (ca. 2.2 Ma); therefore, the use of the term “*Pachycrocuta*-Event” has been proposed to mark the beginning of the Late Villafranchian [7]. Modern studies indicate the diachronic pattern of the settlement of the most widespread forms of large mammals during the transition from the Middle to Late Villafranchian. This has led to an overestimation of the biochronological significance of events based on only one taxon, such as the “Wolf-Event” and “*Pachycrocuta*-Event” [8].

However, the abandonment of the term “Wolf-Event” did not eliminate the great event significance of *Canis* adaptive radiation. The most pronounced increase in the species diversity of the genus in Europe manifested itself during the Calabrian (ca. 1.8–0.8 Ma). From various European sites, the following species described for this interval: *Canis etruscus* Forsyth Major, 1877; *C. arnensis* Del Campana, 1913; *C. mosbachensis* Soergel, 1925; *C. senezensis* Martin, 1973; *C. apolloniensis* Koufos et Kostopoulos, 1997; *C. accitanus* Garrido et Arribas, 2008; *C. borjgali* Bartolini Lucenti et al., 2020; and *C. orcensis* Martínez-Navarro et al., 2021. Recently, *C. senezensis* and *C. accitanus* have come to be considered as junior subjective synonyms of *C. arnensis* [9]. The diagnosis of *C. apolloniensis* (Apollonia, Greece, Late Villafranchian, or Epivillafranchian) is not clearly defined. It is possible that this taxon combines two forms of the genus *Canis*: a smaller one from the group *C. arnensis* and a larger one *C. ex gr. etruscus-mosbachensis*. In particular, according to G. Koufos [10] and our observations, the upper molars of larger *Canis* specimens from Apollonia show characters similar to those of *C. mosbachen-*

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Table 1. Measurements of upper cheek teeth of *Canis etruscus* Forsyth Major, 1877, specimens PIN, nos. 5644/347 and 348; Russia, Crimea, Taurida cave; Lower Pleistocene (L, length; W, width)

Specimen PIN, no.	P1		P2		P3		P4		M1		M2	
	L	W	L	W	L	W	L	W	L	W	L	W
5644/347	7.4*	4.7*	11.6*	4.7*	13.8*	4.8*	20.8	11.8	15.0	19.6	8.6*	12.7*
5644/348	7.5*	4.6*	13.5*	4.5*	16.0*	5.6*	23.3	13.1	14.5*	19.5*	7.6	11.9

* – alveolar measurements.

sis, but not *C. etruscus*. Taking into account the data of recent taxonomic revisions, in this work we provide a comparison with widespread taxa (*C. etruscus*, *C. arnensis*, and *C. mosbachensis*). Particular attention is paid to the recently described species *C. borjgali* from Dmanisi (Georgia, 1.85–1.77 Ma) and *C. orcensis* from Venta Micena (Spain, 1.6–1.5 Ma), which we consider valid on the basis of clearly defined species characters.

The studied material from the Taurida cave is stored at the Borissiak Paleontological Institute of the Russian Academy of Science (PIN), Moscow, Russia. The specimens are two maxillary fragments from two adult individuals (specimens PIN, nos. 5644/347 and 348; collected in 2020, Southern corridor) and a nearly complete dentary with m1 and m2 showing partially worn occlusal surfaces (specimen PIN, no. 5644/349; collected in 2018, Hyena Den site).

Specimens from the type series of *Canis etruscus* and *C. arnensis* from the collection of the Geological and Paleontological section of the Museum of Natural History of the University of Florence (IGF), Italy, were used for comparative analysis. In addition, the described material was compared with the skull of *C. etruscus*, specimen IGF 12334 (on the basis of the cast in the collection of the Geological Institute of the Russian Academy of Sciences, Moscow, Russia). This specimen was established as a lectotype of *C. etruscus* by D. Torre ([11], pl. X, specimen MCM 47; currently IGF 12334, see [12], text-fig. 67B–E). Materials from Untermassfeld in Germany (Research Station of Quaternary Palaeontology (IQW), Weimar) were analyzed [13], as well as specimens of *C. borjgali* from Dmanisi in Georgia (Georgian National Museum (GNM), Tbilisi), personally examined by the authors (M.S. and J.M.-M.).

Representatives of the genus *Canis* demonstrate a high level of morphometric variability (typical for species with a wide range). Therefore, here we used generally accepted persistent dental characters of the species *C. etruscus* [9, 11–17], added by our own observations.

Measurements were made using standard methods. They are given in mm. Designations: Hm1/m2, depth of the dentary between m1 and m2; Hp2/p3, depth of the dentary between p2 and p3; L, length; Lmtst, length of the P4 metastylar lobe; Lta, talonid length;

Ltr, trigonid length; W, width; Wpa, width of the tooth in the paracone area.

The right maxillary fragment, specimen PIN, no. 5644/347 (Figs. 1a, 1b) possesses complete P4 and M1, a partially preserved C1 alveolus and alveoli of P1–P3 and M2. Measurements: LP1–M2, 73.4; LP1–P4, 55.8; LM1–M2, 25.6. The right maxillary fragment, specimen PIN, no. 5644/348 (Figs. 1c, 1d) has P4, M2 and alveoli of P1–P3 and M1. The infra-orbital foramen is located above the posterior root of P3. Measurements: LP1–M2, 77.3; LP1–P4, 59.4; LM1–M2, 24.5. The dimensions of the upper teeth are given in Table 1.

On specimens PIN, nos. 5644/347 and 348 the canine and premolars are not separated by diastemata; a diastema (L, 3.0) is present between P1 and P2 in specimen PIN, no. 5644/347. In *C. arnensis*, diastemata between premolars are always present. In *C. etruscus*, these diastemata are present in most specimens; and this character varies greatly in *C. mosbachensis*. Both examined P4 have a straight buccal margin in occlusal view. The mesial margin of P4 has a weakly defined emargination between the paracone and protocone. The mesial ends of the protocone and paracone are aligned, as in *C. arnensis* and most specimens of *C. etruscus*. The paracone is stout and has a well-defined mesial cutting crest. The protocone prominence is distinct and bears a pronounced cone, unlike *C. orcensis* and *C. lupus*. This conical cusp has two crests, buccolingual and distal. In specimen PIN, no. 5644/347, the buccolingual crest of the protocone does not reach the mesial crest of the paracone, in contrast to specimen PIN, no. 5644/348 (Figs. 1b, 1d). The mesial and lingual cingula are well defined in both specimens, as in *C. arnensis* and *C. etruscus*. The mesiolingual cingulum of the protocone is weakly developed in *C. mosbachensis*, while in *C. lupus* it is absent. In both described specimens, the lingual cingulum lacks a gap at the distal margin of the protocone which is consistent with *C. etruscus* and contrasts with *C. mosbachensis* and *C. lupus*.

The trigon basin on M1 (specimen PIN, no. 5644/347) is larger than the hypocone basin. Both basins are relatively deep, like those of *C. etruscus*, in contrast to the shallower basins of *C. lupus* and *C. borjgali* (specimen GNM, D 1126). The paracone is larger than the metacone in height and area, but the difference in their height is not a big. These cusps are lower

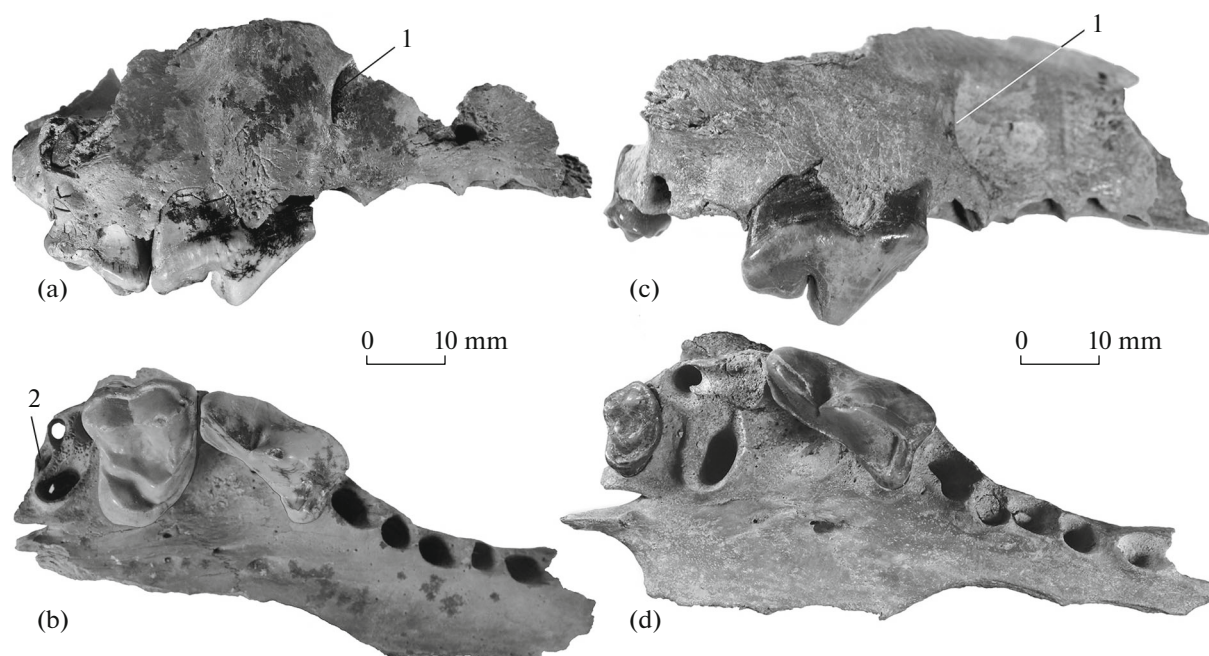


Fig. 1. *Canis etruscus* Forsyth Major, 1877: (a, b) specimen PIN, no. 5644/347, right maxillary fragment with P4–M1, alveoli of C1–P3 and M2: (a) buccal view; (b) occlusal view; (c, d) specimen PIN, no. 5644/348, right maxillary fragment with P4 and M2, alveoli of C1–P3 and M1: (c) buccal view; (d) occlusal view; Russia, Crimea, Taurida cave; Lower Pleistocene. Designations: 1, infraorbital foramen; 2, caudal (fourth) root of M2.

than those of *C. mosbachensis* and *C. lupus*. The tooth is wide mesiodistally, the parastyle is well developed, but its size is smaller than that of the lectotype of *C. etruscus* (IGF 12334). The distal margin of tooth of specimen PIN, no. 5644/347 has a weak flexus. In *C. mosbachensis* and *C. lupus* the flexus is more developed. The inner crest of the paracone (hypoparacrista) is well developed, as in *C. arnensis* and *C. etruscus*. This crest is less pronounced in *C. mosbachensis*, *C. orcensis* and *C. borjgali*. It is completely absent in *C. lupus*. In wolf from the Taurida locality, there is no mesiodistal constriction in the central part of the M1 crown, as in *C. etruscus* and *C. arnensis*. At the same time, in *C. mosbachensis* the tooth constriction is more noticeable, while in *C. lupus* this feature varies. In the specimen from the Taurida cave, M1 has a large protocone, the crista-like metaconule, and the weakly expressed paraconule. The distal crest of the metaconule is connected to the postcingulum. This is corresponded with the characteristics of *C. etruscus*. In

C. mosbachensis and *C. borjgali*, the metaconule is more like a tubercle. The mesiolingual cingulum of M1 on specimen PIN, no. 5644/347 is developed as a wide shelf and without a gap passes into the prehypocrista, as in *C. etruscus*. This cingulum on M1 of *C. orcensis*, *C. mosbachensis*, and *C. borjgali* also does not have a gap, but is much less pronounced. There is no mesiolingual cingulum here in *C. lupus*.

M2 is present only in specimen PIN, no. 5644/348 (Figs. 1c, 1d). On specimen PIN, no. 5644/347, there is only M2 alveolus with canals of four roots, which is unusual for the genus. M2 of specimen PIN, no. 5644/348, it also has four roots. In the occlusal view, M2 has wider and more rounded outlines without a pronounced flexus of the distal margin, in contrast to *C. mosbachensis*. The shape of this tooth is identical to M2 of *C. etruscus* from Olivola (specimen IGF 4411) and Pantalla (Italy; see [16], text-figs. 5a, 5b), and is close to the shape of M2 of the lectotype of *C. etruscus*.

Table 2. Measurements of lower cheek teeth of *Canis etruscus* Forsyth Major, 1877, specimen PIN, no. 5644/349; Russia, Crimea, Taurida cave; Lower Pleistocene (L, length; W, width)

p1		p2		p3		p4		m1		m2		m3	
L	W	L	W	L	W	L	W	L	W	L	W	L	W
5.9*	3.5*	10.7*	4.1*	12.5	5.3	14.2	6.6	25.1	9.5	10.4	8.5	5.2	4.7

* Alveolar measurements.

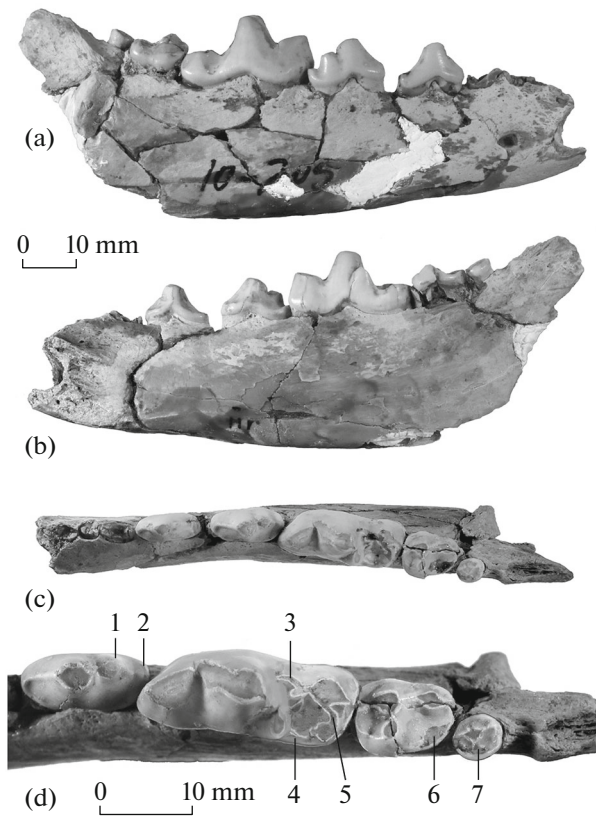


Fig. 2. *Canis etruscus* Forsyth Major, 1877, specimen PIN, no. 5644/349, right dentary with p3–m3 and alveoli of c1–p2: (a) buccal view; (b) lingual view; (c) occlusal view; (d) occlusal view of p3–m3; Russia, Crimea, Taurida cave; Lower Pleistocene. Designations: 1, first accessory cusp of p4; 2, second accessory cusp of p4; 3, protostylid of m1; 4, mesoconid of m1; 5, hypocristid (transversal ridge) of m1; 6, entoconid of m2; 7, metaconid of m3.

In specimen PIN, no. 5644/348, the buccal margins of M1–M2 are located on the same line similar to most *C. etruscus* (for example, specimen IGF 4411 from Olivola). It should be noted that M2 is displaced lingually relative to the buccal margin of M1 in *C. lupus* and this character is rarely present in *C. mosbachensis* from Untermassfeld. The buccal cingulum of M2 is well developed and extends onto the posterior part of the crown, as in other *C. etruscus*. The buccal cusps are low and widely spaced; the paracone is larger in height and area than the metacone. The inner crest of the paracone is well expressed in the basal part. The protocone is large and tall. The metaconule is expressed as a postprotocrista ridge, as in *C. etruscus* and *C. borjgali*. In the contrary, the metaconule of *C. arnensis* is expressed as a tubercle. The metaconule and postprotocrista M2 of *C. mosbachensis* are usually absent. The postcingulum is well developed around the entire posterior part of the tooth. The areas of the trigone and hypocone basins on M2 in the wolf from Taurida cave are equal, as in *C. etruscus*. The area of

the M2 trigon basin of *C. mosbachensis* and *C. borjgali* is larger than the hypocone basin.

The right mandible corpus with p3–m3 and alveoli of c1–p2 (specimen PIN, no. 5644/349; Fig. 2) belongs to an adult individual with moderately worn teeth. The depth of the corpus gradually decreases anteriorly (Hm1/m2, 25.9; Hm1, 27.9; Hp2/p3, 21.0). One large mental foramen has been preserved under the anterior root of p2. All teeth are tightly adjacent to each other, there is a diastema (L, 1.8) only between p3 and p4. Dentition lengths: Lp1–m3, 84.6; Lp1–p4, 46.2; Lm1–m3, 39.4. In buccal view, all the bases of the premolar crowns are at the same level with the basal line of the m1; this feature is character primarily for the earliest representatives of the genus *Canis* (*C. etruscus* and *C. arnensis*). In occlusal view, a small buccolingual flexion of the dentition is between p4 and m1. The posterior end of p4 overlaps the anterior end of m1 in an echelon-like manner, similar to *C. etruscus* (lectotype IGF 12334). On the contrary, the dentition is straight in the holotype of *C. arnensis* (IGF 869) and there is no overlap of the crowns of p4 and m1.

The alveolus of single-rooted p1 is tightly adjacent to the canine alveolus. Crowns of p2–p4 are buccolingually narrow and slightly asymmetrical, with well-developed crests (cristids). The lingual margin of p3 in occlusal view is almost straight, the accessory cusp is absent, the postcingulid is developed in the form of a distinct distal ridge, and the lingual cingulid is weak (as in lectotype IGF 12334). The first distal accessory cusp of p4 is proportionally large; the second accessory cusp is developed in the form of a distinct ridge-like elevation, separated from the postcingulid (Fig. 2d). The lingual cingulid is moderately developed along the entire crown side; the buccal cingulid is weakly expressed.

The metaconid of m1 is large and well individualized. Its apex is displaced distal to the protoconid and deflected lingually relative to the dorsoventral axis of the tooth (it corresponds to the morphology of *C. etruscus*, in particular to the lectotype IGF 12334). The distal crest of the metaconid (metacristid) is expressed only at its base, where it connects with the mesial crest of the entoconid (Fig. 2d). Unlike most *C. etruscus*, the described specimen from Crimea has a small mesoconid in front of the entoconid; the mesoconid closes the talonid basin lingually, as in *C. orcenis* and most specimens of *C. mosbachensis*. The specimen from the Taurida locality has a well-defined protostylid on the mesiobuccal part of the tooth similar to most *C. etruscus*. The talonid width of m1 is about 95% of the trigonid width. The buccal flexid is not expressed (unlike *C. mosbachensis* and *C. lupus*); on talonid, the hypocristid (transversal ridge [12]), connecting the hypoconid and entoconid, is well developed. The base of the hypoconid is significantly wider than the base of the entoconid. The lingual cingulid is

weak, it expressed from the line of the metaconid apex to the distal margin of the crown; a weak lingual cingulid is also present at the base of the paraconid.

The crown of m2 has a subrectangular occlusal outline, its talonid is mesiodistally short and buccolingually wide, and has two distinct cusps (Fig. 2d). The paraconid is ridge-like, the protoconid and metaconid are located on the same transverse line. The talonid width is approximately 88% of the trigonid width. The hypoconid is large, the entoconid is tubercle-like, low. The mesiobuccal cingulid and distobuccal cingulid (under the hypoconid) are well developed (it is the plesiomorphic character). The outline of the tooth in occlusal view and the presence of two cusps on the talonid correspond to the m2 morphology in the type series of *C. etruscus*. The talonid tapers distally in *C. mosbachensis*, *C. borjgali*, and *C. orcensis*, unlike *C. etruscus*. In the first three species, a cristid-like elevation is often developed (in particular, in specimens D-1, D-646, D-2917, etc., of *C. borjgali* from Dmanisi and in the majority of *C. mosbachensis* from Unter-massfeld) instead of the distolingual cusp (entoconid) characteristic of *C. etruscus* [13].

The ultimate lower molar m3 is displaced lingually from the longitudinal axis of the dentition. Due to the presence of a developed talonid basin, it has an elliptical outline in occlusal view. The cingulid is developed along the entire perimeter of the tooth. The main cuspid (protoconid) is displaced buccally, it has mesial and distal crests oriented mesiodistally. There is a small, well-defined metaconid lingual to the protoconid, and on the same transverse axis with it. The lingual side of the metaconid is connected to the cingulid. The m3 metaconid of *C. mosbachensis* is much less developed; in *C. lupus* there is the only cuspid on m3 which located in the center of the tooth. The m3 of *C. borjgali* displays two distinct cuspids (the protoconid is larger), connected by crests, but the outline of the tooth is more rounded than in *C. etruscus*. In addition, *C. etruscus*, *C. lupus*, and *C. mosbachensis* have cingulid around the entire m3 (*C. borjgali* has only precingulid and postcingulids).

The first half of the Calabrian (ca. 1.8–1.2 Ma) in Europe was a time of climatic stability characterized by a predominance of open environments and some aridity phases that preceded a non-linear phase of glacial cyclicity, featured by significant amplitude and asymmetry, which began approximately at 1.2 Ma, marking the ‘Early-Middle Pleistocene Transition’. Representatives of the tribe Canini became widespread during this time, accompanied by an extraordinary increase in the biodiversity of recorded taxa associated to open landscapes. It is generally assumed that at this time occurred the first dispersal in Europe of the three main groups of canids: the medium-sized wolf-like forms (*C. etruscus* and *C. mosbachensis*), the jackal-like *C. arnensis*, and the large forms with signs

of hypercarnivorous dental specialization represented by the genus *Xenocyon* Kretzoi, 1938.

C. orcensis from Venta Micena and *C. borjgali* from Dmanisi do not differ in size from other wolf-like forms [18, 19]. The last two species are based on the description of a several finds from single localities, so comparison with these taxa in this study is preliminary, unlike *C. etruscus* and *C. mosbachensis*, which are well-known from a plethora of European localities. Morphological analysis of *C. etruscus* from classical European localities indicates relatively high intraspecific variability. The main tendency of hypocarnivorous specialization in the entire hypodigm of *C. etruscus* is well expressed [11, 12, 15–17].

Our analysis showed that the specimens from the Taurida cave, in terms of morphometric features and morphological characters (in particular, characters associated with the hypocarnivory specialisation), belong to *C. etruscus*. On the lower teeth of the wolf from Crimea, characters of hypocarnivory include: a strong and lingually deviated metaconid, a well developed protostylid on m1; m2 mesiodistally long and buccolingually wide with subsquare occlusal outline and a developed entoconid region with a distinct cuspid; m3 is proportionally large, elliptical in outline with a developed talonid basin. Hypocarnivorous features of upper teeth include: buccolingually wide and relatively low crowns of M1–M2, which are practically devoid of distal flexi and have occlusal subsquare rather than subtriangular outlines; the protocone prominence of P4 is well developed with a well-defined cone. Specially noteworthy is the presence of four roots on M2 for the described form from the Taurida cave. This is a rare feature in *Canis*. It indirectly indicates a tendency towards a hypocarnivorous direction in the development of molars. Comparison with other species of genus (*C. orcensis*, *C. mosbachensis*, *C. borjgali*) suggests that the development of these taxa was typical for the time of adaptive radiation of this group of wolf-like species, which formed intermediate characters directed towards the development of wolves of the *C. lupus* group, appeared during the Middle Pleistocene.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

Fossil materials were examined. No live animals were used in the study.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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