

Cheetah *Acinonyx pardinensis* (Felidae, Carnivora) from the Early Pleistocene of Crimea (Taurida Cave)

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Abstract—A mandible fragment of *Acinonyx pardinensis* (Croizet et Jobert, 1828) is described from the Early Pleistocene locality in the Taurida cave (Crimea, Late Villafranchian, about 1.8–1.5 Ma). This is the first discovery of the genus *Acinonyx* in the Pleistocene of Crimea. Along with other felids, such as *Homotherium*, *Megantereon*, *Panthera*, *Lynx*, and *Puma*, cheetahs were typical representatives of the Late Villafranchian faunas of Eurasia. In the Taurida locality, *Acinonyx pardinensis* is co-occurred with *Homotherium crenatidens*, *Megantereon adroveri*, and *Lynx issiodorensis*.

Keywords: *Acinonyx pardinensis*, felids, Late Villafranchian, Taurida cave, Crimea

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The genus *Acinonyx* Brookes, 1828 appears in the fossil record at approximately 4 Ma in Africa [1, 2]. The dating agrees with molecular genetic data, which indicate that the lineage of cheetahs and cougars, including modern *Acinonyx jubatus* (Schreber, 1775), *Puma concolor* (Linnaeus, 1771), and *P. yagouaroundi* (Geoffroy, 1803), originates from the Early Miocene and that *Acinonyx* and *Puma* diverged in the Early Pliocene (within 5–4 Ma) [3, 4]. Finds of two species of the genus *Acinonyx*, *A. pardinensis* (Croizet et Jobert, 1828) and *A. jubatus*, are known from Africa. In the Early Pleistocene, *A. pardinensis* was widespread in Eurasia as well [5]. Fossil finds assigned to *A. jubatus* are known only from Africa and date back to 3.0–1.8 Ma (although the species assignment of certain finds is questionable) [2, 6].

Like modern *A. jubatus*, *A. pardinensis* was most likely capable of reaching a high running speed due to unique locomotor adaptations of the genus *Acinonyx*. However, *A. pardinensis* was far greater than *A. jubatus* in body size and weight (60–120 kg) and could hunt prey weighing up to 100 kg [2]. There is an opinion that

all Pleistocene finds of *Acinonyx* from Eurasia belong to *A. pardinensis* [2, 5, 7, 8]. However, recent studies [9] have shown that *A. pardinensis* inhabited Eurasia in the Late Pliocene and most part of the Early Pleistocene (2.8–1.3 Ma), while *A. pleistocaenicus* (Zdansky, 1925), which is the largest representative of the genus, lived in Eurasia at the end of Early Pleistocene and the beginning of Middle Pleistocene (1.3–0.6 Ma) [9]. The relatively small species *A. intermedius* Thenius, 1954 has been found to occur in Eurasia within a short time interval in the Middle Pleistocene (approximately 0.5 Ma) [9].

Apart from *Acinonyx*, other felids of more than 10 kg in weight inhabited Europe in the Late Villafranchian, representing the genera *Homotherium*, *Megantereon*, *Panthera*, *Lynx*, and *Puma* [9, 10]. The animals differed in their adaptations and shared the trophic niche of large carnivores, and cheetahs were most likely efficient in competing with the other felids.

The abundant Late Villafranchian vertebrate fauna from the Taurida cave of central Crimea has been dated to the Early Pleistocene (MQ1, approximately 1.8–1.5 Ma) [11]. Felids of the Taurida cave are represented by *Homotherium crenatidens* (Fabrini, 1890), *Megantereon adroveri* Pons-Moyà, 1987, *Lynx issiodorensis* (Croizet et Jobert, 1828) [12], and the *A. pardinensis* find described below. *Acinonyx* fossils have not been found in Crimea earlier, and only two *A. pardinensis* finds from Russia have been known from Early Pleistocene (Khaprovian) localities of the Northern Azov region [13].

The described material from the Taurida cave is a fragment of the right dentary (specimen IPAE, no. 727/2261, collection of 2022). The specimen is stored in the museum of the Institute of Plant and

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Table 1. Measurements of m1 and dentary depth (mm) in *Acinonyx pardinensis* (Croizet et Jobert, 1828) and *Puma pardoides* (Owen, 1846). Designations: H/m1, depth of the dentary behind m1; Lm1, length of m1; Lm1pa, length of m1 paraconid; Lm1pr, length of m1 protoconid; Wm1, width of m1. Abbreviations: IGF, Museum of Paleontology, University of Florence, Florence, Italy; IPS, Catalan Institute of Palaeontology Miquel Crusafont, Sabadell, Spain; IQW, Research Station of Quaternary Palaeontology, Weimar, Germany; StV, collection from Saint-Vallier, Musée des Confluences, Lyon, France

Species	Locality	Collection, specimen	Lm1	Wm1	Lm1pa	Lm1pr	H/m1
<i>A. pardinensis</i>	Saint-Vallier	IPS 17102 QSV1126	20.06	11.49	10.60	10.10	21.74
<i>A. pardinensis</i>	Saint-Vallier	StV 272	19.00	9.60	10.10	8.90	25.80
<i>A. pardinensis</i>	Saint-Vallier	StV 20161828	20.70	10.60	10.50	11.80	29.10
<i>A. pardinensis</i>	Saint-Vallier	StV 161822	19.00	10.90	10.20	11.95	26.50
<i>A. pardinensis</i>	Saint-Vallier	StV 161822	19.80	11.10	9.10	11.50	27.30
<i>A. pardinensis</i>	Saint-Vallier	StV 20161819	18.50	9.30	10.10	9.20	26.00
<i>A. pardinensis</i>	Untermassfeld	IQW 1980/15503	23.90	10.30	11.20	10.50	33.00
<i>A. pardinensis</i>	Untermassfeld	IQW 1980/15503	23.40	10.00	11.10	10.20	32.80
<i>A. pardinensis</i>	Villarroya	IPS 35087	21.44	8.86	12.41	11.37	29.54
<i>A. pardinensis</i>	Taurida cave	IPAE, no. 727/2261	20.90	9.50	10.70	12.10	24.30
<i>P. pardoides</i>	Cueva Victoria	IPS 4144	18.59	8.90	11.26	7.59	–
<i>P. pardoides</i>	Puebla Valverde	IPS 36127	19.80	8.90	12.40	8.50	–
<i>P. pardoides</i>	Saint-Vallier	StV 161854	18.70	8.30	10.50	9.10	28.30
<i>P. pardoides</i>	Saint-Vallier	StV 161853	15.60	7.60	6.60	8.80	23.40
<i>P. pardoides</i>	Saint-Vallier	StV 161855	18.40	8.00	8.70	9.10	27.70
<i>P. pardoides</i>	Saint-Vallier	StV 137	16.30	7.80	9.80	8.50	–
<i>P. pardoides</i>	Saint-Vallier	StV 138	18.90	8.20	10.06	8.98	–
<i>P. pardoides</i>	Stránská skála	no number	17.00	8.40	–	–	–
<i>P. pardoides</i>	Tasso FU	IGF 851	22.10	10.10	12.30	11.60	34.30
<i>P. pardoides</i>	Untermassfeld	IQW 1983/18556	16.90	7.90	10.50	8.20	26.00
<i>A. pardinensis</i>	Etouaires	IPS 17126 M-15	24.37	10.58	11.92	12.67	30.96

Animal Ecology (IPAE), Yekaterinburg. Comparisons were performed with *A. pardinensis* specimens collected from the Villafranchian localities Etouaires, Saint-Vallier (France), Untermassfeld (Germany), and Villarroya (Spain) and stored in the Catalan Institute of Palaeontology Miquel Crusafont (IPS), Sabadell, Spain; the collection from Saint-Vallier (StV), Musée des Confluences, Lyon, France; and the Research Station of Quaternary Palaeontology (IQW), Weimar, Germany. In addition, we studied the *Puma pardoides* (Owen, 1846) finds collected from the Villafranchian localities Puebla Valverde, Cueva Victoria (Spain), Tasso FU (Italy), Stránská skála (Czech Republic), Saint-Vallier, and Untermassfeld and stored in the above collections and the Museum of Paleontology (IGF), University of Florence, Florence, Italy.

Measurements accurate to 0.01 mm were performed with a caliper according to a published technique [9]. Principal component analysis and plotting were carried out using Past 4.0 (Syntel Studio).

The fragment of the right dentary (specimen IPAE, no. 727/2261) contains unworn m1 and a part of the posterior root alveolus of p4; the anterior part of the horizontal ramus is lost; the ascending ramus is broken at the foramen mandibulae level. The mandibular foramen is high and has a rounded anterior margin. A margin of the attachment area of the musculus temporalis pars medialis is well defined and prominent on the medial side of the base of the coronoid process. The anterior part of this margin reaches the level of the posterior protrusion of m1; the temporalis muscle attachment area relief does not extend ventrally. The horizontal ramus of the mandible is sufficiently deep and robust in the region preserved. The anterior part of the fossa masseterica ascends smoothly and has a subdued relief. The anterior margin of the masseteric fossa is somewhat distal to the posterior end of m1.

The lower carnassial tooth m1 is robust; the anterior wall of the paraconid slopes backward; the carnassial notch is well defined. The protoconid is higher and more massive than the paraconid. The enamel is

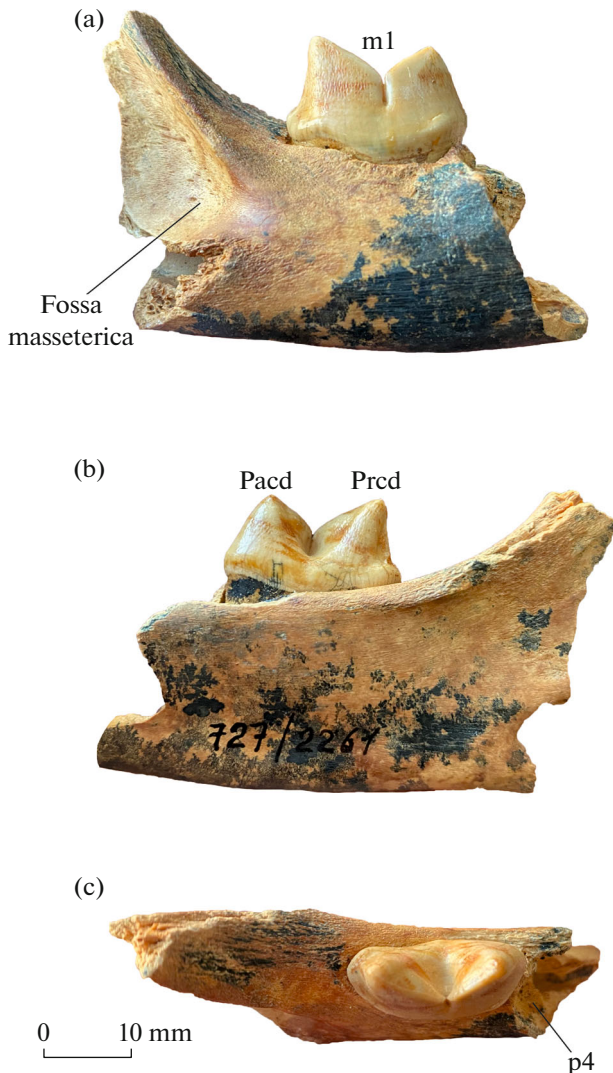


Fig. 1. *Acinonyx pardinensis* (Croizet et Jobert, 1828), specimen IPAE, no. 727/2261, right dentary fragment: (a) buccal view, (b) lingual view, (c) occlusal view; Crimea, Taurida cave; Lower Pleistocene. Designations: m1, lower carnassial tooth m1; p4, posterior root alveolus of the ultimate lower premolar p4; Pacd, paraconid of m1; Prco, protoconid of m1.

crenulated on the buccal and lingual sides of the tooth. A short, but distinct cingulid is found under the paraconid on the labial side and in the posterior part of the crown on the lingual side. The posterior protoconid blade is distinct and splits at the base. A distinct protrusion is seen in the posterior part of the crown base and resembles a rudimental talonid. There is a slight prominence on the lingual wall of the crown base, between the paraconid and protoconid, opposite the carnassial notch (an occlusal view); the lingual margin is clearly bent distal to the prominence.

The dimensions of m1 and the mandible are summarized in Table 1.

Machairodontinae members can be excluded from comparisons because of substantial differences in m1 shape and dimensions (see [14, 15]). The measurements of m1 and the mandible in *Lynx issiodorensis* [16] do not overlap the respective parameters of Pleistocene cheetahs [9]. The earliest remains of *Panthera pardus* (Linnaeus, 1758) in Europe originate from the Lower Pleistocene of the Vallonnet Cave (France; approximately 1.2 Ma); a leopard has not been detected in older deposits [17].

Acinonyx pardinensis and *Panthera gombaszoegensis* (Kretzoi, 1938) inhabited Europe simultaneously during the Early and Middle Pleistocene; their fossils have been found together in at least seven localities [8]. Although *Panthera gombaszoegensis* has been larger in size than *A. pardinensis*, m1 is sometimes rather small in panthers [18, 19] and its dimensions fall within the variation range of m1 dimensions in cheetahs. However, the smallest known *Panthera gombaszoegensis* individuals, which are from the L'Escaie locality, France, already have an appreciably greater depth of the dentary behind m1 (range 26.2–33.0 mm, $n = 6$ [18]) as compared with *A. pardinensis* from the Taurida cave (24.3 mm, see Table 1).

In view of the above, the dimensions (m1 length, m1 width, m1 paraconid length, m1 protoconid length, and depth of the dentary behind m1) of *A. pardinensis* were compared with those of *Puma pardoides*, a Pleistocene medium-size felid species that is quite similar to cheetahs both morphologically and genetically. A sample distribution in the space of the two first principal components is shown in Fig. 2. As is seen, *A. pardinensis* specimens form a cloud, which has no overlap with a *Puma pardoides* cloud. Specimen IPAE, no. 727/2261 from the Taurida locality is within the distribution area of the *A. pardinensis* specimens and substantially away from the *Puma pardoides* area.

Morphologically, m1 of specimen IPAE, no. 727/2261 has minor similarities to *Puma pardoides* (see [20]), having a high protoconid and a substantial slope of the anterior wall of the paraconid. Based on other characteristics, m1 of specimen IPAE, no. 727/2261 corresponds to *A. pardinensis*. The characteristics include the following: m1 is more robust, a posterior protrusion in the base of the posterior wall of the protoconid is greater, and the prominence and the curvature of the lingual margin of the crown base are distinct. A prominence between the paraconid and protoconid in the lingual part of the m1 crown is found in 85–90% of *A. pardinensis* individuals [9].

Generally, m1 tends to be wider in *A. pardinensis* and narrower in *Puma pardoides*. The mandible is more gracile and has a low horizontal ramus in *Puma pardoides*, while the *A. pardinensis* mandible is more robust and deeper. Thus, specimen IPAE, no. 727/2261 from the Taurida cave displays all features necessary for its reliable attribution to *A. pardinensis*. The find supplements the composition of the large carnivore

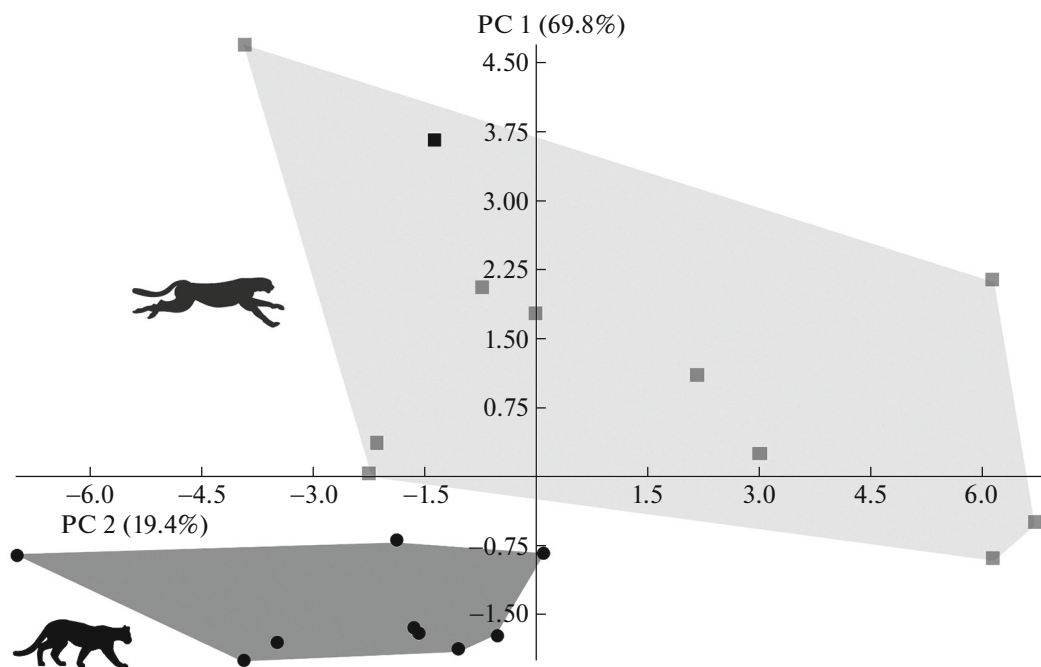


Fig. 2. Distribution of *Acinonyx pardinensis* (Croizet et Jobert, 1828) and *Puma pardoides* (Owen, 1846) samples (see Table 1) in the space of the two first principal components. Black circles, *P. pardoides*; gray squares, *A. pardinensis*; black square, specimen IPAE, no. 727/2261 from the Taurida cave.

guild of the Taurida cave fauna and provides the first evidence that cheetahs have inhabited Crimea in the Early Pleistocene.

CONFLICT OF INTEREST

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

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

Only fossil materials were used in this work. This work does not contain any studies involving live animal subjects.

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