Journal of Iberian Geology (2021) 47:535–549
https://doi.org/10.1007/s41513-021-00164-1

RESEARCH PAPER

First record of *Pachycrocuta brevirostris* (Gervais, 1850) from Ukraine on the background of the European occurrence of the species

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Received: 23 July 2020 / Accepted: 18 January 2021 / Published online: 11 February 2021

Abstract

Cranial material of *Pachycrocuta brevirostris* from the late Early Pleistocene site of Nogaisk is the first record of this species in Ukraine. This large hyena was a representative of the Tamanian faunal complex and a single specialised scavenger in these faunas. The revisited European records list of *P. brevirostris* documented the presence of this species in 101 sites, dated in the range of 3.5–0.4 Ma. This species first disappeared in Africa, survived in Europe until ca. 0.8–0.7 Ma, and its last, relict occurrence was known from south-eastern Asia. The main reason of extinction of *P. brevirostris* probably was the competition with *Crocuta crocuta*. The cave hyena was smaller, but its teeth were proportionally larger to the body size, better adapted to crushing bones and slicing meat, and could also hunt united in larger groups.

Keywords Nogaisk · Maxilla · Competition · Occurrence · Extinction · Nogaisk · Maxilar · Competencia · Ocurrencia · Extinción

Resumen

El material craneal de *Pachycrocuta brevirostris* de la localidad de Nogaisk del final del Pleistoceno inferior es el primer registro de esta especie en Ucrania. Esta gran hiena es un representante de los carnívoros del complejo faunístico de Tamania y el único carroñero especializado. La lista revisada de registros europeos de *P. brevirostris* documentó la presencia de esta especie en 101 yacimientos datados entre 3.5-0.4 Ma. Esta especie desapareció primero en África, pero sobrevivió en Europa hasta ca. 0.8-0.7 Ma, y su último relicto se conoció en el sudeste asiático. La principal razón de la extinción de *P. brevirostris* fue probablemente la competencia con *Crocuta crocuta*. La hiena de las cavernas era más pequeña, pero sus dientes eran proporcionalmente más grandes al tamaño del cuerpo por lo que estaban mejor adaptados para triturar huesos y rebanar carne, y también podían unirse en grupos más grandes para cazar.

Palabras clave Nogaisk · Maxilar · Competencia · Ocurrencia · Extinción

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1 Introduction

The Tamanian faunal complex was firstly established by Gromov (1948) based on the presence of large mammals as one of the biochronological units of the East European Pleistocene (Vislobokova and Titov 2020). After the description of the type site, which is Sinyaya Balka on the Tamanian Peninsula in Russia (Gromov 1948), a number of new mammal localities of this complex have been discovered there and within the north-eastern coastal area of the Sea of Azov in Russia, Azerbaijan and Georgia (Vereshchagin, 1957, 1959; Dubrovo 1963; Alekseeva 1977; Vangengeim et al. 1991; Baigusheva 2000; Tesakov 2004; Dodonov et al. 2006; Tesakov et al. 2007, 2013; Baigusheva and Titov 2008; Bukhsianidze et al. 2014; Vislobokova and Titov 2020).

Based on biostratigraphic and paleomagnetic data, the time range of the Tamanian complex sense strict was estimated as ca. 1.2–0.87 Ma (MIS 36 to the MIS 22–21 boundary, equivalent of Western European Epivillafranchian). It approximately corresponds to the interval between the Cobb Mountain paleomagnetic Subchron and the Brunhes/Matuyama Chron boundary (Markova 2007; Vislobokova and Tesakov 2013; Markova and Vislobokova 2016; Vislobokova and Titov 2020). The key species of the Tamanian complex is *Mammuthus* (*Archidiskodon*) *meridionalis tamanensis* Dubrovo, 1964. Other characteristic herbivores includes *Equus* aff. *suessenbornensis* Wüst, 1901, *Stephanorhinus etruscus* (Falconer 1868), and *Elasmotherium caucasicum* Borissiak, 1914 (Gromov 1948; Vereshchagin 1957; Dubrovo and Alekseev 1964; Alekseeva 1977; Vislobokova and Titov 2020). Among carnivores, the most important taxa include *Canis mosbachensis tamanensis* (Vereshchagin 1957), *Lycaon lycaonoides* (Kretzoi 1938), *Lutra simplicidens* Thenius, 1965, *Homotherium latidens* (Owen 1846), *Acinonyx pardinensis* Croizet and Jobert, 1828, and *Pachycrocuta brevirostris* Gervais, 1850 (Sotnikova et al. 2002; Titov 2008; Sotnikova and Titov 2008).

Stone artefacts from Sinyaya Balka document one of the oldest Palaeolithic human occurrences in Europe (Shchelinsky et al. 2010). In this context, the study of Tamanian faunas is of particular interest for the reconstruction of the ancient human settlement and environment at that time (Vislobokova and Titov 2020). This task requires a revision of faunal lists from particular sites previously assigned to the Tamanian complex, especially the composition of large mammals, as possible resource and competitor species for the Palaeolithic humans (Vislobokova and Titov 2020).

Although different carnivore species for the Tamanian faunal complex from Ukraine were listed in a number of publications (e.g., Topachevsky 1965; Vereshchagin et al. 1971; Kahlke 1975), they have not been properly revised. In this respect, old collections and newly collected materials require a substantial revision and analysis. The main purpose of this article is the re-study of hyena material from Nogaisk stored in the National Museum of Natural History in Kyiv and Zaporizhzhia Regional Local History Museum. Several skull fragments were found on the coast of the Sea of Azov in 1979. Recently it was possible to combine all remains for our study. The individual from Nogaisk locality provided the first occurrence of *P. brevirostris* in the modern territory of Ukraine. Additionally, the study provides a new evidence on morphology and evolution of this species within Eurasia.

2 Locality and stratigraphy

A few high coastal sections along the Taganrog Gulf shore expose subaqual sediments such as fluviatile deposits of ancient Don River origin and estuarine deposits of the Sea of Azov. These sediments are overlain by subaerial deposits that primarily belong to the loess-paleosol formation. The underlying subaqual deposits are arranged in three terraces, with the earliest one, the Nogaisk terrace yielding fossil remains of mammals of the Tamanian faunal assemblage. The two others, the Platovo and Voznesenskaya terraces, contain a fauna corresponding to the Middle Pleistocene (Velichko et al. 2010).

The Nogaisk locality is located on the northern coast of the Sea of Azov near Primorsk village (Zaporizhzhia Oblast, Ukraine), 2.5–3 km to the east from Obitochna foreland. The association of small and large mammals from this locality is characterised mostly by ancient forms, among which only a few were present in the Middle Pleistocene. As for the species list, a significant bias was established for this locality. Large animals are very rarely found, and their remains are usually fragmentary and in bad condition, whereas small mammal remains are quite abundant and well preserved. Fossils were found in a complex of abandoned channel and lacustrine sediments. Two layers, sometimes described as two sites (Nogaisk 1 and 2) were distinguished, but contained the same fauna and were contemporary (Rekovets and Nadachowski 1996; Kowalski 2001). Deposits consisted mainly of layered, partly ferrugineol clayey sand and gravel with small carbonate concretions and/or sandstone pebbles (Kovalchuk et al. 2017).

The mammal assemblage includes 33 species: *Erinaceus* sp.; *Desmana nogaica* Topachevsky and Pashkov, 1990; *Spermophilus nogaici* (Topachevsky 1957); *Trogontherium cuvieri* Fischer von Waldheim, 1809; *Castor fiber* Linnaeus, 1758; *Sicista vinogradovi* Topachevsky 1965; *Sicista* sp.; *Borsodia newtoni* (Forsyth Major, 1902); *Clethrionomys* *kretzoii* (Kowalski, 1958); *Allocricetus ehiki* Schaub, 1930; *Cricetus cricetus* (Linnaeus 1758); *Ellobius palaeotalpinus* Schevtschenko, 1965; *Lagurodon arankae* (Kretzoi 1942); *Mimomys rex* Kormos, 1934; *Mimomys reidi* Hinton, 1910; *Mimomys savini* Hinton, 1910; *Plioscirtopoda stepanovi* Schevchenko, 1965; *Prolagurus pannonicus* Kormos 1930; *Pygerethmus pumilio* (Kerr, 1792); *Spalax minor* Topachevsky 1965; *Lepus* sp.; *Ochotona* sp.; *Canis* sp.; *Mustela stromeri* Kormos, 1934; *Mustela palerminea* (Petenyi 1864); *Mustela praenivalis* Kormos, 1934; *Pachycrocuta brevirostris* (Gervais 1850); *Mammuthus meridionalis* (Nesti 1825); *Equus* aff. *suessenbornensis* Wüst, 1901; *Elasmotherium caucasicum* Borissiak, 1914; *Megaloceros* sp.; *Bison* sp.; *Pontoceros ambiguus* Vereshchagin et al. 1971 (Topachevsky 1957; Garutt 1954; Kretzoi 1965; Topachevsky 1965; Vereshchagin et al. 1971; Kahlke 1975; Garutt and Foronova 1976; Dubrovo and Kapelist 1979; Topachevsky et al. 1987; Garutt et al. 1990; Rekovets 1994; Rekovets and Nadachowski 1996; Kowalski 2001; Velichko et al. 2010; Popescu 2011; Kolfschoten and Markova 2005; Rekovets et al. 2009; Maschenko et al. 2011; Larramendi 2016; Vislobokova and Titov 2020).

Rekovets and Nadachowski (1996) noted that the predominant species from Nogaisk, constituting up to 60% of the micromammal assemblage, were representatives of genera *Lagurodon*, *Allophaiomys* and *Spermophilus*. Other taxa belonging to *Ellobius* (common), Spalacidae or Cricetidae (rarer) retained ancestral, morphological characters. Allactaginae were diverse, but not very common, also as *Spalax* and *Prolagurus* forms (Rekovets and Nadachowski 1996). Lagurid molars with a "*praepannonicus*" morphology (broadly confluent triangles T4–T5) prevail in earlier faunas. The mean value of the ratio of anteroconid complex length to the total length of the first lower molar from Nogaisk equals 47.7, which suggests an older age than e.g. Zapadnye Kairy (mean value of this index for m1 of *Prolagurus* is 50.0) (Rekovets 1994; Kolfschoten and Markova 2005). The Nogaisk micromammal assemblage is characterised by the appearance of *Prolagurus pannonicus* and progressiveness of *Allophaiomys pliocaenicus*, which is recorded in the change of molar morpho structure pattern. The main indexes of this evolutional level are as follows: anteroconid complex to the total tooth length is 42–44, and the SDQ (Schmelzband-Differenzierung-Quotient, molar enamel thickness) is 90–100. The evolutionary stage of *Prolagurus pannonicus* resembles forms from the Tamanian faunal assemblage. Primitive morphotypes of *Mimomys* also indicate the similar age (Velichko et al. 2010). Based on all these data, the fauna from Nogaisk is dated to the late Early Pleistocene, between ca. 1.2–1.1 Ma. It is correlated with an early Tamanian faunal complex (Iosifova and Agadjanian 2010; Krokhmal 2010; Velichko et al. 2010; Kovalchuk 2017).

3 Material and methods

The identification of *P. brevirostris* was performed using basic morphometric analysis. Measurements were taken point to point, with an electronic calliper to the nearest 0.1 mm. Each value given here is the mean of three measurements (all in mm). The mean is rounded to one decimal digit. Measuring schemes and morphological terminology were taken and modified from Barycka (2008). Throughout the text, upper teeth are referred to using capital letters (e.g. P4), and lower teeth with lowercase letters (e.g. p4).

The material comprises a few skull fragments of a very large hyena, and all listed remains belong to a single adult individual with slightly worn teeth (Fig. 1). The specimen NMNHU-P 27–1689 is a fragmentary right half of the skull, including a part of the maxilla with I2 and P2-M1, zygomatic arch, palatine and broken basicranium. It is stored in the collection of the Department of Vertebrate Palaeontology (National Museum of Natural History, National Academy of Sciences of Ukraine). The second skull fragment is in the collection of Zaporizhzhia Regional Local History Museum under collection no. P-446/KV-23356. It is the right premaxilla with alveoli of I1 and I3 and including P2 and a part of maxilla with alveoli of P1–P2.

Fig. 1 Cranial fragment of *Pachycrocuta brevirostris* from Nogaisk (Ukraine) NMNHU-P 27–1689 in buccal view (top) and occlusal view (bottom, scale bar 5 cm). Photo by Y. Semenov

4 Systematic palaeontology

4.1 Description

The studied skull was previously classified as *Hyaena* sp. (Topachevsky 1965). The palatine fissure is placed approximately at an angle of 17° to the sagittal line of the skull (Fig. 1). The major palatine foramen is located in the middle part of maxillary palatine process, at the level of the P3 anterior root. The anterior border of the incisura palatine posterior is placed 23 mm behind the line connecting the caudal ends of P4. The length from prosthion to posterior border of hard palate is 173 mm, width at the canines is ca. 80 mm, and ca. 150 mm between the labial surfaces of P4. The zygomatic arch is very robust: the depth of the zygomatic bone anterior to its frontal process is 50 mm, while the maximum depth of the zygomatic process of the temporal bone is 58 mm. The tube of the external auditory meatus is moderately long and pressed closely against the caudal surface of the postglenoid process.

The tooth row is moderately curved, and the incisors are separated from the canine by a relatively long diastema. Shorter diastemas are present between C1 and P1 and P1 and P2, while P2-M1 are tightly appressed. All teeth are large and moderately worn (Fig. 1, Table 1). The I1 alveolus is large and narrow, and strongly flattened laterally. The preserved I2 is a large, strongly laterally flattened tooth, with a strong main cusp with its tip directed distally. Distal to the main cusp, on the distal edge, two smaller, symmetrically positioned cusplets are present. Wear produces an even plane across the apex. Judging from the I3 alveolus, this incisor was canine-like and much larger than the other two incisors. The oval shape of the alveolus shows that C1 was very large, massive and appreciably flattened. The oval P1 alveolus shows a small, reduced tooth, shifted medially in the tooth row. The two-rooted and rectangular P2 is a broad and low crowned tooth, with relatively short and low main cusp (paracone). The mesial and distal margins of the crown are blunt, while the buccal and lingual margins are more or less straight, and slightly curved only in the distal part. Only a delicate concavity of the buccal and lingual sides occurs in the middle part of the crown, in the transition between the mesial and distal portions of the tooth; the transition is slightly marked. The small and low anterior accessory cusplet, the protocone, is shifted moderately mesio-lingually, and weakly associated with the main cusp. It is separated from the paracone by a deep, narrow, V-shaped valley. After the paracone, the posterior accessory cusplet, the hypocone, is placed almost at the midline of the tooth. It is larger than the protocone, but also low and separated from the paracone by a shallow and wide valley. The crocutoid P3 is a massive and moderately high, almost rectangular tooth. It possesses a short and high paracone, which occupies 2/3 the crown length. The mesial, distal and lingual margins of the crown are rounded, while the buccal margin is mostly straight. There are notable concavities in the median part of the crown, in the well-marked transition between the anterior and posterior parts of the tooth. A rudimentary, vestigial anterior cusplet, the protocone, is shifted mesio-lingually. A thin but well-defined ridge runs from its base to the apex of the paracone. The posterior accessory cusplet, the hypocone, is located just behind the main cusp; it is larger than the protocone, and differentiated from the paracone by a deep and V-shaped valley. A crescent-like, shallow, U-shaped valley is present in the disto-lingual part of the crown, between the paracone and the cingulum ridge. A posterior ridge, connecting the hypocone with the apex of the paracone, is sharply pointed and less visible than the anterior ridge. The entire crown is collared by a thick cingulum, which is weakly developed on the buccal side. There is a wide, shallow, U-shaped valley between the cingulum ridge and the paracone on the bucco-mesial and mesial side; it forms a large crescent in occlusal view.

The P4 has a triangular, moderately-developed, relatively narrow and low protocone with centrally positioned tip. Its mesial margin is rounded, and the cusp is situated at an angle of 80° to the rest of the tooth, and is somewhat forwardly sloped. In occlusal view, the tooth is elongated and narrow, with a convex buccal margin and abruptly ending crown narrowing distally. In buccal view, the tooth looks low. The parastyle is large, high and oval. It is well separated from the paracone by a deep and sharply pointed notch, and the constriction between the parastyle and the paracone is noticeable in occlusal view. The anterior wall of the parastyle bears a small but well-defined preparastyle, which forms a vertical ridge on the mesial side, and is connected with an anterior cingulum. The paracone is relatively low and short, while the metastyle is longer than the paracone. Paracone and metastyle form almost continuous cutting surface; there is only a shallow notch between them. The tooth displays a basal triangle where the strong mesialo-lingual keel joins the cingulum. Perpendicularly oriented to the rest teeth, two-rooted M1 is functionally retained and moderately reduced.

Table 1 Measurements of *Pachycrocuta brevirostris* from Nogaisk (all in mm)

Character	P2	P3	P4	M1
Total length	21.0	27.3	40.8	6.2
Paracone length	12.5	18.2	12.3	
Metastyle length			14.4	
Anterior breadth	12.9	19.3	24.0	
Posterior breadth	14.0	19.7	13.2	
Total breadth				13.9

Its oval trigon is collared with a high and thin cingulum wall, and the trigon base is developed into a broad and shallow surface. The talon is more reduced and narrower, and connected with the P4 metastyle.

4.2 Comparisons

The above described, partially preserved skull belonged to a very large hyena, and its fragmentary condition made taxonomic attribution difficult. However, thanks to mainly complete tooth row and moderately worn teeth, it is possible to provide a clear taxonomic affiliation. From this time interval (late Early Pleistocene) in Eastern Europe, the presence of three large hyenas should be taken acknowledged: *Pachycrocuta brevirostris*, *Pliocrocuta perrieri* (Croizet and Jobert 1828), and possibly *Crocuta crocuta* ssp. Perhaps, a fourth, large hyena species, *Chasmaporthetes lunensis* Del Campana 1914 was present there. However, *C. lunensis* vanished much earlier, with its last Eurasian appearance documented from the German site Schernfeld dated to 1.8–1.6 Ma (Qiu 1987; Turner et al. 2008; A.M. pers. obs.). In addition, the teeth of this species are distinctly smaller and narrower than those in the specimen from Nogaisk. As for *P. perrieri*, the examined individual from Nogaisk also cannot be attributed to this species. The size of Nogaisk hyena exceeds the values known for *P. perrieri*, where P3 length does not reach 26.0 mm, and P4 length does not exceed 38.0 mm (Schütt 1972; Kurtén 1972; Kurtén and Poulianos 1977, 1981).

Only a hypothetical presence of *C. crocuta* in Nogaisk could be proposed, even if this species appeared in European faunas much later, ca. 0.8 Ma in Trinchera Dolina (Madurell-Malapeira et al. 2014). *P. brevirostris* is regarded as the largest hyena ever existed, approaching the size of a female lion, *Panthera leo* (Linnaeus 1758), with an average weight of ca. 110–120 kg, and the maximal weight up to 180 kg (Turner and Antón 1996; Turner 2001; Palmqvist et al. 2011). This is twice the weight of the extant spotted hyena, and much larger than the Middle and Late Pleistocene *Crocuta crocuta spelaea* Goldfuss, 1823. Large teeth were often regarded in the past as a diagnostic feature of the large body size. However, contrary to the canines or the first lower molar (m1), the upper carnassials (P4) are not useful for determining the sexual dimorphism or body size. Their measurements are not correlated with those of the body. As remarked by Lundholm (1952): "…the animal may have been comparatively small, as compared with other members of the same population, however small individuals have had relatively bigger teeth than those in larger specimens". Other possibly important factors that may affect the size of the teeth are climatic and geographical factors, sexual dimorphism and changes over time, which further complicates the interpretation of such data. Contrary to Ursidae, Felidae, and Mustelidae, and partially similarly to Canidae, Hyaenidae are virtually monomorphic in linear measurements, and sexual dimorphism can be cautiously rejected. Comparison of large subspecies of the cave hyena *Crocuta crocuta praespelaea* with *P. brevirostris* reveals that the latter possesses in average a larger and narrower P4 with proportionally short metastyle. Beside the size, the present teeth differ also in various diagnostic characters such as a relatively low P3 crown (more brachydont) with stronger hypocone and the development of a triangular surface between the paracone and the strong cingulum ridge on the medio-lingual side. The main cusp is proportionally shorter and lower. The P4 of the Nogaisk hyena differs from P4 of *C. crocuta* in the presence of well-developed preparastyle, larger parastyle, which is better separated from the paracone, broader blade and proportionally shorter metastyle. Less reduced M1, with a size (13.9 mm) exceeding for *C. crocuta*, in which this tooth is rarely larger than 8 mm. The C1 alveolus is still informative even if the tooth is missing. Its length (25.4 mm) and width (16.1) exceed the diameters obtained for the very large Middle Pleistocene cave hyenas from Mosbach 2 or Petralona cave (Schütt 1971; Kurtén 1972; Kurtén and Poulianos 1977, 1981). For these reasons, we attribute the analysed specimen from Nogaisk to *P. brevirostris*.

5 Discussion

Pachycrocuta brevirostris is first recorded in South Turkwel (northern Kenya, Africa) ca. 3.6–3.5 Ma (Werdelin 1999; Werdelin and Lewis 2000, 2005, 2008), Laetoli ca. 3.5 Ma (Leakey and Hay 1979; Arribas and Palmqvist 1999), West Turkana sites LO5 and LO10 (3.5–3 Ma), possibly Koobi Fora, Tulku Bor Mb (3.4–2.6 Ma). This species was also recorded in Makapansgat (ca. 3.1–3.0 Ma; Howell and petter 1979, 1980; Randall 1981; Arribas and Palmqvist 1998, 1999). The earliest Asian record from Nihowan is slightly younger and dated to ca. 2.0 Ma (Teilhard de Chardin and Piveteau 1930).

Their ancestors likely evolved from the late Miocene *Hyaenictitherium* (Howell and Petter 1980). *P. brevirostris* coexisted with *Crocuta* in Africa during more than 1 million years, and disappeared in East Africa in the Late Pliocene but dispersed and was still present in Southern Africa (Toerien 1952; Randall 1981; Werdelin 1999), where it was recorded among others in Sterkfontein 4–5 (2.6–2.4 Ma; Howell and Petter 1980; Turner 1987; Turner and Antón 1996), Bolt's Farm (2.5–2.3 Ma; Mutter et al. 2001). *P. brevirostris* is still present in southern Africa during the middle and late Early Pleistocene, and their remains were found in Kromdraai A (1.6–1.5 Ma; Ewer 1954; Howell and Petter 1980; Turner 1987) and Swartkrans 3 (1.5–1.4 Ma; Mutter et al. 2001). The latest African record of the species is known from the Gladysvale cave (1.1–1.0 Ma; Mutter et al. 2001).

The Early Pleistocene records of this hyena from Central and Eastern Asia are common: (1) Pinjor Formation (2.5–2.4 Ma; Arribas and Palmqvist 1999); (2) Mohui (2.5–2.4 Ma; Louys 2014); (3) Djetis (2.0–1.9 Ma; Dubois 1908; Schütt 1972; Geraads 1979); (4) Tologoi (2.0–1.8 Ma; Turner and Antón 1996); (5) Volga river (2.0–1.5 Ma; Turner and Antón 1996); (6) Kopaly (1.6–1.5 Ma; Kojamkulova et al. 1987; Sotnikova et al. 1997; Vislobokova 2005); (7) Liucheng (1.2–1.0 Ma; Louys 2014); (8) Zasukhino (1.1–1.0 Ma; Sotnikova 1989; Turner and Antón 1996); (9) Gongwangling (1.1–1.0 Ma; Louys 2014); (10) Lakhuti (1.1–1.0 Ma; Sotnikova and Vislobokova 1990; Turner and Antón 1996); (11) Nalaikcha (1.1–1.0 Ma; Sotnikova 1989; Turner and Antón 1996). *P. brevirostris* has become quite rare in Asia already in the early Middle Pleistocene and present only in the south-eastern and eastern parts of the continent, being recorded for this period from Bukuran, Ngebung level B and Kedung Brubus, all dated on 0.9–0.8 Ma (Bouteaux et al. 2007; Bouteaux and Moigne 2010; Louys 2014). The species survived during the late Middle Pleistocene, with the latest occurrence at Zhoukoudian 1, dated on 0.5–0.4 Ma (Turner and Antón 1996; Boaz et al. 2000, 2004; Dennell et al. 2008).

During the Early Pleistocene, the species reached Europe (most probably from Asia) (Werdelin 1999; Palmqvist et al. 2011). In a short time, *P. brevirostris* replaced two other large hyaenid species, the large bone-crushing *Pliocrocuta perrieri* and the gracile pack hunter *Chasmaporthetes lunensis* (Turner and Antón 1996; Turner et al. 2008). It was present in Europe between 2.0 and 0.7 Ma, and finally disappeared during the early Middle Pleistocene (Fig. 2; Table 2; Turner and Antón 1996; Arribas and Palmqvist 1999; Turner et al. 2008; Palmqvist et al. 2011).

The extinction of *P. brevirostris* in Europe was probably linked to the decline and subsequent extinction of sabertooth cats, particularly *Megantereon whitei* and *Homotherium crenatidens* (Martínez-Navarro and Palmqvist 1996; Palmqvist et al. 1996a, b; Palmqvist and Arribas 2001a, b; Palmqvist et al. 2011). Disappearance of these cats implied the loss of an important source of partly consumed carcasses and thus a change in the interactions between flesh-eating and bone-crushing species of the carnivore guild.

P. brevirostris was a member of the large carnivore paleoguild comprising also *Lycaon falconeri/lycaonoides*, *Canis etruscus/mosbachensis*, *Ursus etruscus/arctos*, *H. crenatidens/latidens*, *M. whitei*, *Panthera toscana/gombaszoegensis*, *Acinonyx pardinensis*, *Puma pardoides*, and *Lynx issiodorensis/pardinus*. This carnivore assemblage existed in Eurasia for more than one million years (between 2.0 and 0.9–0.8 Ma), and its paleohierarchy was more or less stable. Thanks to its large size and social lifestyle, *P. brevirostris* was one of the dominant species (Turner and Antón 1996; Turner 2001; Palmqvist et al. 2011).

Nevertheless, the evolutionary history of this species was ended during the latest Early Pleistocene, where *P. brevirostris* was replaced by *C. crocuta*. The earliest European records of this species are known from Spanish sites at the Gran Dolina of Atapuerca (García 2003). In general opinion, Trinchera Dolina 4 (TD4) is dated to the Early-Middle Pleistocene boundary (ca. 0.78 Ma). However, new ESR dates suggest that the age of this horizon is closer to 0.9 Ma, whereas Trinchera Dolina 4 (TD4) is close to the Jaramillo subchron (Moreno-García 2011; Madurell-Malapeira et al. 2014). This new chronological background suggests co-existence in time of *P. brevirostris* and *C. crocuta* in the Iberian Peninsula during the latest Early Pleistocene

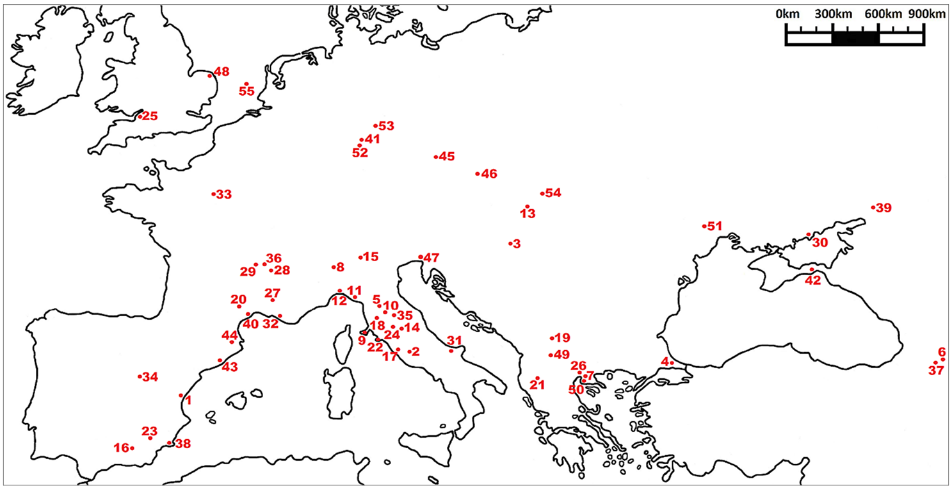

Fig. 2 Distribution of Plio-Pleistocene sites with *P. brevirostris* in Europe and adjoining areas. For locality numbers – see Table 2

Table 2 Occurrence of *P. brevirostris* in the Plio-Pleistocene of Europe and adjoining areas. Locality numbers (Map) correspond to those in Fig. 2

Map	Site	Age (in Ma)	Literature
1	Almenara-Casablanca 1	2.0–1.8	Soto and Morales 1985; Agusti and Moyà Solà 1998; Madurell-Malapeira et al. 2014
2	Coste San Giacomo	2.2–2.0	Biddittu et al. 1979; Bellucci et al. 2012
3	Beremend 15	2.6–2.4	Jánossy 1987
4	Yassioren	2.4–2.2	Ozansoy 1965
5	Cassa Frata	1.9–1.8	Borselli et al. 1980; De Giuli and Masini 1986; Caloi and Palombo 1995; Turner et al. 2008
5	Casa Sgherri (Massarella)	1.9–1.8	Turner et al. 2008
6	Dmanisi	1.9–1.8	Palmqvist et al. 2011
7	Gerakarou	1.9–1.8	Kostopoulos et al. 2002; Koufos and Kostopoulos 2016
8	Olivola	1.9–1.8	Azzaroli 1977, 1983; Turner et al. 2008
9	Poggio Rosso	1.9–1.8	Alberdi et al. 1998; Mazza et al. 2004
10	Tasso	1.9–1.8	Alberdi et al. 1998
5	Upper Valdarno	1.9–1.8	Del Campana 1914; Bonifay 1971; Azzaroli et al. 1988; Torre et al. 1993; Rook et al. 2013
11	Val di Magra	1.9–1.8	Forsyth Major 1890; Gliozzi et al. 1997
12	Villa Spinola	1.9–1.8	Tuccimei 1896; Bortolotti 1903 1905; Argenti 2004
13	Kisláng	1.9–1.7	Kretzoi 1954; Jánossy 1986; Turner and Antón 1996
14	Cava est Casigliano	1.8–1.7	Argenti 2004
15	Casale Violino	1.8–1.7	Ambrosetti et al. 1995; Argenti 2004
16	Fonelas P-1	1.8–1.7	Garrido 2006; Viseras et al. 2006; Arribas and Garrido 2008; Arribas et al. 2009
17	Fontana Acetosa	1.8–1.7	Caloi and Palombo 1995; Kahlke et al. 2011
18	Colle Saint Andrea	1.8–1.7	Argenti 2004
19	Trlica	1.8–1.6	Dimitrijević 1990; Dimitrijević et al. 2006; Vislobokova and Agadjanian 2015
20	Hérault	1.6–1.5	Crochet et al. 2009
21	Livakkos	1.6–1.5	Steensma 1988; Koufos and Kostopoulos 1997; Koufos 2014
22	Monte Argentario	1.6–1.5	Baschieri and Serge 1957
23	Venta Micena	1.6–1.5	Pons-Moyà 1987; Martínez-Navarro 1992; Palmqvist et al. 1996a, b, 2003, 2005, 2011; Medin et al. 2017
15	Leffe Basin	1.6–1.4	Breda and Marchetti 2007
24	Paciano	1.6–1.4	Argenti 2004
23	Barranco León 5	1.5–1.4	Turq et al. 1996; Martínez-Navarro et al. 2003, 2004, 2010
25	Westbury-sub-Mendip	1.5–1.4	Bishop 1982, Turner 1995, 1999, 2009
26	Tsiotra Vryssi	1.5–1.3	Konidaris et al. 2015
27	Sartanette	1.5–1.3	Bonnet 1980, Palombo and Valli 2004
28	Escoffier	1.5–1.1	Fourvel and Lateur 2016
23	Fuente Nueva 3	1.4–1.3	Turq et al. 1996; Martínez-Navarro et al. 2003, 2010; Espigares et al. 2013;
7	Kalamoto	1.4–1.3	Tsoukala and Chatzopoulou 2005; Konidaris et al. 2015
7	Apollonia 1	1.3–1.2	Koufos and Kostopoulos 1997; Koufos 2018
29	Ceyssaguet	1.3–1.2	Tsoukala and Bonifay 2004; Argant and Bonifay 2011
30	Nogaisk	1.3–1.2	Topachevsky 1965
31	Pirro Nord	1.3–1.2	De Giuli et al. 1986; Turner et al. 2008; Petrucci et al. 2013
20	Bois-de-Riquet	1.3–1.1	Crochet et al. 2009; Bourguignon et al. 2016
27	Grosse Marguerite cave	1.3–1.1	Fourvel and Lateur 2016
32	Trois Pigeons	1.3–1.1	Fourvel and Lateur 2016
33	Saint-Prest	1.2–1.0	Guérin 1980; Guérin et al. 2003; Palombo and Valli 2004; Guérin 2007
34	Pontón de la Oliva	1.1–1.0	Cabra et al. 1983; Sesé and Ruiz-Bustos 1992; Madurell-Malapeira et al. 2014
35	Promano	1.1–1.0	Argenti 2004
36	Sainzelles	1.1–1.0	Aymard 1846; Boule 1893; Guérin 1980, Alba et al. 2015
37	Akhakalaki 1	1.1–1.0	Martinez-Navarro et al. 2009

Table 2 (continued)

Map	Site	Age (in Ma)	Literature
38	Cueva Victoria	1.1–0.8	Pons-Moyà and Moyà-Solà 1978; Agustí et al. 1986; Aguirre 1989; Madurell-Malapeira et al. 2015
39	Liventsovka	1.1–1.0	Sotnikova et al. 2002; Titov 2008; Sotnikova and Titov 2009
40	Vallonnet cave	1.1–1.0	de Lumley et al. 1988; Moullé 1992, 1998; Moullé and Tréguier 2006
41	Untermassfeld	1.1–1.0	Kahlke 2000; Turner 2001; Kahlke and Gaudzinski 2005
42	Akhtanizovskaya	1.1–0.9	Sotnikova and Titov 2009
43	Cal Guardiola Lower Unit	1.2–1.1	Madurell-Malapeira et al. 2009a, 2009b, 2010, 2014
44	Incarcal	0.9–0.8	Galobart et al. 2003
43	Vallparadís Estació Lower Unit	1.0–0.9	Madurell-Malapeira et al. 2009a, 2009b, 2010, 2014, 2015, 2017
43	Cal Guardiola Upper Unit	0.9–0.8	Madurell-Malapeira et al. 2009a, 2009b, 2010, 2014, 2015, 2017
45	Prezletice	0.9–0.8	Fejfar 1995; Koenigswald and Heinrich 1999
46	Chlum 1	0.8–0.7	Beneš 1970; Horáček et al. 2016
46	Chlum 4	0.8–0.7	Beneš 1970; Horáček et al. 2016
47	Slivia	1.0–0.9	Ambrosetti et al. 1979, 1995; Turner and Antón 1996; Caloi and Palombo 1995
43	Vallparadís Estació Middle Unit	0.85–0.8	Madurell-Malapeira et al. 2009a, 2009b, 2010, 2014, 2015, 2017
48	Bacton	0.8–0.7	Bishop 1982; Lewis et al. 2010
48	Forest Bed	0.8–0.7	Lewis et al. 2010
45	Koneprusy C718	0.8–0.7	Turner and Antón 1996
49	Manastirec	0.8–0.7	Kurtén and Garevski 1989
48	Mundesley	0.8–0.7	Bishop 1982; Turner 1995, 1999
50	Petralona cave	0.8–0.7	Kurtén and Poulianos 1977, 1981; Baryshnikov and Tsoukala 2010
48	Overstrand	0.8–0.7	Lewis et al. 2010
48	Sidestrand	0.8–0.7	Freudenberg 1914; Bishop 1982; Lewis et al. 2010
45	Stránská skála	0.8–0.7	Stehlík 1934; Kurtén 1968, 1972; Musil 1995
51	Tiraspol	0.8–0.7	Pavlow 1925; Nikivorova et al. 1971; Godina and David 1973
52	Würzburg-Schalksberg	0.8–0.7	Schütt 1974; Mäuser 1987; Turner et al. 2008
49	West Runton	0.75–0.7	Turner 2009; Lewis et al. 2010; Stuart and Lister 2010
53	Süssenborn	0.8–0.7	Soergel 1936; Kahlke 1961; Schaefer 1969
54	Gombaszög	0.8–0.7	Kretzoi 1938, 1941
55	Brown Ridge	?	Erdbrink and van Bree 1995

(Madurell-Malapeira et al. 2014). This should not be surprising, since the co-existence of these two hyaenids is well documented for more than one million years in East Africa (Werdelin and Lewis 2005). Although it should be noted that the African *C. crocuta* that co-existed with *P. brevirostris* was a much smaller and gracile species than the European Middle Pleistocene form (Madurell-Malapeira et al. 2014).

It is interesting that *P. brevirostris* disappeared more or less simultaneously in most of Europe, and survived only in Western and Central Europe (Turner and Antón 1996; Turner 2001; Palmqvist et al. 2011). But even there sites younger than 0.7 Ma are unknown. The only exception is the Hungarian site Vertesszöllös 2, but the presence of this species is based on questionable remains (Jánossy 1990). Also, some admixture of older layers also cannot be excluded (Burdukiewicz pers. comm.). Numerous species, like *L. lycaonoides* or *P. gombaszoegensis*, which co-occurred with *P. brevirostris*, survived in Central and Eastern Europe longer, even until the late Middle Pleistocene (MIS 11–10) (Jánossy 1990; Baryshnikov 2011; Marciszak 2014). The exact answer for this difference is unknown and needs further research.

P. brevirostris disappeared relatively fast likely due to the competitive pressure from *C. crocuta*, but the exact reconstruction of this scenario is still unresolved. It is known that, despite its larger body size, *P. brevirostris* has proportionally smaller teeth than *C. crocuta*, which was not only better adapted for bone crushing (proportionally wider and larger P3 and p3), but also for slicing the meat. Upper carnassials (P4) of *P. brevirostris* had a proportionally shorter metastyle (cutting blade) and narrower crown, while its lower carnassials (m1) were smaller (compared to body size) with shorter major cusps (Turner and Antón 1996; Turner 2001; Barycka 2008). Both species are characterised by other adaptations to bone crushing like zigzag-like enamel structure (Stefen and Resenberger 2002, Barycka 2008). In aggressive encounters one to one, *C. crocuta* had likely no chance against *P. brevirostris*, but *C. crocuta* lived and hunted in larger clans than *P. brevirostris* (Turner and Antón 1996; Turner 2001; Barycka 2008; Palmqvist et al. 2011). These two reasons, better adaptation for crushing bones and meat slicing and more numerous clans, were probably the main factors responsible for the success of *C. crocuta*. However, other factors might also have played some role in this process. As was pointed by Vinuesa et al. (2016), the ancestral/plesiomorphic condition in bone-crushing hyenas were limited social behavior with putative main scavenger behavior (i.e. similar to extant brown hyenas). The extreme social behavior displayed by the extant spotted hyenas probably was related with unknown selective pressures occurred during the Middle Pleistocene in East Africa or idiosyncratic biological characteristics of this species. Taking this into account, the scenario discussed above showed not to be so clear and still needs further verification (Vinuesa et al. 2016).

The first Ukrainian record described here, dated to 1.3–1.2 Ma, fits well into this scenario. Beside the single record from Ubeidyia, dated to 1.5–1.4 Ma (Martínez-Navarro et al. 2009), there are no other known Eastern European or Western Asian records of *C. crocuta*. In this context, the co-occurrence *P. brevirostris* with *C. crocuta* seems unlikely in this area, but needs further investigation. Specimens of *P. brevirostris* from various earlier sites located in neighbouring areas to the so called "Khapry fauna" of Nogaisk are morphologically similar to the Asian forms. This might indicate that *P. brevirostris* may have appeared in Eastern Europe earlier than in western regions (Sotnikova et al. 2002). In general, the Asian influence on the fauna of the Azov region was reasonably strong. Apart from carnivores, which appeared here earlier than in Western Europe by the invasion from the east, the Khaprovian faunal assemblage consists of typical Asian elements (Sotnikova et al. 2002).

Acknowledgements We are very grateful to Oleksandr Kovalchuk for linguistic improvements and to two anonymous reviewers for their insightful comments and remarks, which significantly improved the manuscript. The research was financed from the subsidies for the activities of the Institute of Environmental Biology, University of Wrocław, no. 2020 (501).

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