Zoodiversity, **57**(2): 151–170, 2023
DOI 10.15407/zoo2023.02.151

Paleontology

UDC 568.26 [551.793.9] (477.55)

ONE OR TWO: HOW MANY SPECIES OF THE GENUS *PYRRHOCORAX* (PASSERIFORMES, CORVIDAE) INHABITED THE CRIMEA DURING THE LATE PLEISTOCENE?

L. Gorobets[1]*, O. Kovalchuk[1,2] & B. Ridush[3]

[1]*Department of Palaeontology, National Museum of Natural History NAS of Ukraine, B. Khmelnytsky St., 15, Kyiv, 01054 Ukraine*
[2]*Department of Palaeozoology, Faculty of Biological Sciences, University of Wroclaw, Sienkiewicza St., 21, Wroclaw, 50-335, Poland*
[3]*Department of Physical Geography, Geomorphology and Palaeogeography, Yuriy Fedkovych Chernivtsi National University, Kotsubynskogo St., 2, Chernivtsi, 58012 Ukraine*
**Corresponding author*
E-mail: ornitologist@gmail.com

L. Gorobets (https://orcid.org/0000-0002-5492-7878)
O. Kovalchuk (https://orcid.org/0000-0002-9545-208X)
B. Ridush (https://orcid.org/0000-0002-5896-6073)

urn:lsid:zoobank.org:pub:3F2343F9-4007-4E99-AD88-ABBCDBA322F2

One or Two: How Many Species of the Genus *Pyrrhocorax* (Passeriformes, Corvidae) Inhabited the Crimea During the Late Pleistocene? Gorobets, L., Kovalchuk, O. & Ridush, B. —The article provides an overview of bird remains assigned to the genus *Pyrrhocorax* Tunstall, 1771 from nine cave sites of Late Pleistocene and Early Holocene age within the Crimean Peninsula (Ukraine). A large sample of chough bones from the Emine-Bair-Khosar Cave (722 bones) is processed and the results obtained are presented here for the first time. Re-identification of the remains revealed the presence of the Alpine chough *Pyrrhocorax graculus* in the studied region instead of two species of the genus *Pyrrhocorax* as previously believed. The material processed was assigned to an extinct subspecies, *Pyrrhocorax graculus vetus*, based on a series of measurements taken from various skeletal elements (in particular, coracoideum, humerus, ulna, radius, carpometacarpus, femur, tibiotarsus, and tarsometatarsus). The previous assumptions of the coexistence of two chough species in the Crimea during the Late Pleistocene made it possible to consider climate in this region as relatively warm. Our results indirectly revealed that the climate of the Crimean Peninsula at the verge of the Late Pleistocene and Holocene was rather cool and therefore unsuitable for the red-billed chough.
Key words: Alpine, cave sites, bone morphology, morphometry, Quaternary, Europe.

Introduction

Numerous fossil bird remains of Late Pleistocene age were found in sediments filling caves and rock shelters in the Crimean Peninsula (Tugarinov, 1937; Voinstvensky, 1963, 1967; Baryshnikov & Potapova, 1988, 1992; Gavris & Taykova, 2004; Tsvelykh, 2013, 2017, 2018; Majkić et al., 2017; Kovalchuk et al., 2021). During Pleistocene glaciations, this area could have been a refugium for many species including birds, which subsequently settled in the southern part of Eastern Europe (Nikiforov, 2008). The study of Late Pleistocene fossil remains from the Crimean Peninsula is one of the keys to understanding the history of the avifauna of Eastern Europe. Nowadays, most of the bird species identified in the Late Pleistocene of the Crimea are common not only within this peninsula, but in the entire territory of Ukraine. Nevertheless, several species have disappeared from the region, including representatives of the genus *Pyrrhocorax* Tunstall, 1771, the remains of which were numerous among Late Pleistocene birds. They were not recorded in the Crimea for 200 years of zoological observations (Kostin, 2006).

Several publications on the study of Pleistocene birds of the Crimea appeared in the 20th century (e. g., Tugarinov, 1937; Voinstvensky, 1963, 1965, 1967; Baryshnikov & Potapova, 1988). Authors of these articles mentioned two species, *Pyrrhocorax pyrrhocorax* and *P. graculus*, which coexisted there during the Late Pleistocene. However, the methods used by these researchers raise doubts about the accuracy of the species identification. A critical analysis of past publications and the study of new finds are crucial for establishing a correct number of species of the genus *Pyrrhocorax* lived in the territory of the Crimea in the Late Pleistocene. These bird species often coexist in ecosystems, but their habitats differ substantially. The Alpine chough *Pyrrhocorax graculus* prefers high mountain rocky areas and tolerates cold conditions (Madge, 2019). In these birds, survival rate in winter is higher than in summer, and warming during cold seasons negatively affects the number of adults (Chiffard et al., 2019). The red-billed chough *Pyrrhocorax pyrrhocorax* also inhabits mountainous regions, although it can nest at the sea level (McKay, 1996). Throughout the year, the diet of the latter species includes mainly insects (Laiolo & Rolando, 1999), so these birds avoid extremely cold conditions. Accurate information about the coexistence of two species of the genus *Pyrrhocorax* or, vice versa, the presence of only one of them is important for better understanding paleoecological conditions in the Crimea.

The aim of this paper is to present the results of a revision of a large sample of chough remains (including those described for the first time) from the Late Pleistocene of the Crimean Peninsula.

Fossil record of the genus *Pyrrhocorax*

All known fossil bird remains of the genus *Pyrrhocorax* belong to the extant species — the red-billed chough *Pyrrhocorax pyrrhocorax* (Linnaeus, 1758) and the Alpine chough *P. graculus* (Linnaeus, 1766). A single extinct species, *Pyrrhocorax primigenius*, was described by Milne-Edwards (1875) from the Pleistocene of France. However, Mourer-Chauviré (1975) re-examined the type series of this species and came to the conclusion that *P. primigenius* does not deserve the species rank and rather represents an extinct subspecies of the nominal species: *Pyrrhocorax pyrrhocorax primigenius* (Milne-Edwards, 1875), based on differences in size of the bones (Mourer-Chauviré, 1975). Mlíkovský (2002) believed the using subspecies categories for extinct birds is not substantiated enough and referred the chough bones from France as *P. pyrrhocorax*. An extinct subspecies *Pyrrhocorax graculus vetus* Mourer-Chauviré, 1975 was described for the Alpine chough. The previously used *Pyrrhocorax graculus vetus* Kretzoi, 1962 is considered to be *nomen nudum* (Mlíkovský, 2002; Kurochkin et al., 2015).

The extant *Pyrrhocorax graculus graculus* (Linnaeus, 1766) inhabits mountainous regions in Europe and North Africa; bones of this subspecies now predominate in comparative osteological collections of Europe (Cramp & Perrins, 1994). *P. graculus graculus* differs from *P. graculus vetus* in size: long tubular bones of the latter are shorter and thicker (Mourer-Chauviré, 1975). The size of skeletal elements in extinct and extant subspecies has a significant overlap. Identification of fossils usually requires a large sample or the finding of bones with sizes that are reliably different from those in extant birds. This is probably one of the reasons why most researchers avoid describing new subspecies.

The range and time of existence of *Pyrrhocorax graculus vetus* is insufficiently studied. This subspecies is recorded in the Late Pliocene, Early and Late Pleistocene of Hungary, Early and Middle Pleistocene of Romania, and Late Pleistocene of Austria and Slovakia (Kessler, 2020). In our opinion, in this case, the identification of a subspecies does not have a proper argumentation. In each locality, the sample is not significant (usually less than 10 specimens including phalanges), the bones are damaged, and it is possible to take only a few measurements. In addition, Kessler (2020) mentioned the Late Pliocene finds of the *P. graculus vetus* remains with reference to Jánossy (1972), although corvids are not mentioned at all in the article cited. In addition to the type locality (Saint-Estève) and other Middle Pleistocene localities in France (Mourer-Chauviré, 1975), *P. graculus vetus* has been identified in materials from the Late Pleistocene locality of Devetashka Cave in Bulgaria (Boev,

1999) and Treugolnaya Cave in the North Caucasus (Potapova & Baryshnikov, 1993). Numerous remains of this subspecies were found in Bulgaria (number of identifiable specimens — 197), the sample from the Caucasus is smaller (number of identifiable specimens — 23), but the measurements provided indicate a high probability that the subspecies is identified correctly.

The earliest finds of bird remains of the genus *Pyrrhocorax* are described from the Csarnóta 2 locality in Hungary, dated to the Early Pliocene (Kessler, 2013, 2020; Kessler & Horváth, 2022). Nevertheless, this information needs confirmation (Kurochkin et al., 2015). The place of their deposition is not specified. During the re-identification of bird remains described in the above articles, a large number of errors were found, including the identification not only to the species or genus, but also to the family and even order level (see Zelenkov, 2016 a, b, 2017 for more details).

Reliable finds of *Pyrrhocorax* are known from the Late Pliocene, both in the east and west of Europe, in Bulgaria (Boev, 2000) and Spain (Villalta, 1964), respectively. Probably, two species of this genus could have been found in the Late Pliocene, although researchers preferred describing them in open nomenclature as either *P.* cf. *pyrrhocorax* or *P.* aff. *pyrrhocorax*. During Pleistocene, *P. graculus* and *P. pyrrhocorax* were quite numerous in mountainous regions of southern Europe (south of 50° N latitude). Remains of these species were found in dozens of Pleistocene localities in western, central and eastern parts of the subcontinent (Tyrberg, 1998; Boev, 1999; Mlíkovský, 2002). The easternmost finds of Early Pleistocene age are confined to Bulgaria (Boev, 2006 a: only *P. pyrrhocorax*) and Romania (Čapek, 1917; Jánossy, 1979: both species), i. e. westward of the Crimea. During the Middle Pleistocene, both species of the genus *Pyrrhocorax* existed further east of the Crimea, in the North Caucasus (Potapova & Baryshnikov, 1993; Baryshnikov & Potapova, 1995). In most localities, remains of both these species have been identified, although only *P. graculus* is usually described from Eastern Europe (Tyrberg, 1991; Boev, 1994; Mlíkovský, 1997; Wojtal et al., 2012). Such a difference can be explained by cooler conditions in this part of Europe during that time (Tyrberg, 1991). There are data on the coexistence of *P. graculus* and *P. pyrrhocorax* in the Late Pleistocene of the Crimea (Tugarinov, 1937; Voinstvensky, 1967; Baryshnikov & Potapova, 1988), but we doubt the accuracy of these identifications. Voinstvensky (1967) published a survey of Miocene–Holocene birds of Ukraine but he does not specify how he recognized these two extant species. Tugarinov (1937) and later Baryshnikov & Potapova (1988) described their methodology although there are grounds for skepticism. These authors described the same sample (number of identifiable specimens — 209), but their results differ significantly (see below). The authors have not commented the reason for such a great discrepancy. We believe that the information on the number of *Pyrrhocorax* species in the Pleistocene of the Crimea needs to be re-examined.

Material and Methods

The material for this study comes from nine cave sites in the Crimean Mountains (fig. 1). Almost all the remains described (except some specimens from Sjuren 1 and Adzhi-Koba Caves) are deposited in the collection of the Department of Palaeontology, National Museum of Natural History (NMNHU of the National Academy of Sciences of Ukraine in Kyiv, and they were re-identified by one of us (LG). For most of the localities listed below (except of Emine-Bair-Khosar), the age was determined by accompanying archaeological artifacts. A mixing of layers of different age has been established for some of these sites, which was not previously considered. In particular, the remains of *Gallus gallus* were described from the Late Palaeolithic of Kara-Koba (Voinstvensky, 1967); this is not possible, chickens appeared in Europe much later (Best et al., 2022). Anatomical terminology presented here follows Baumel et al. (1993). Most of the measurements were taken according to the scheme in Tomek & Bochenski (2000), in some cases according to Mourer-Chauviré (1975) which is indicated separately.

Studied localities

Emine-Bair-Khosar (44°48'04.65" N, 34°17'21.99" E). The cave (fig. 2) is situated on the north edge of the Chatyrdag Plateau, which is a part of the Main Range of the Crimean Mountains. It is a complex 125 m deep karst shaft, consisting of subvertical and subhorizontal parts, with a total length of 1485 m. The several sites with bone remains are concentrated in the upper part, to a depth of 50 m. The main way of the large mammals' bone accumulation was through the vertical 18-meter-deep entrance pit, which functioned as a trap. At the same time, scavengers could penetrate to the cave through another entrance, leading via the subhorizontal gallery (the Northern Gallery), to the pit bottom (Vremir & Ridush, 2005; Ridush et al., 2013). The entrance pit is 4-meter-wide in its mouth, widening into an extensive chamber (the Main Chamber), up to 20 m wide and up to 15 m high. Because of the wide entrance, more than half of this chamber is in the photic zone. Therefore, the alpine choughs, as well as the other troglophilous bird species, could be nesting in the niches in walls and ceiling. Even in the present days, the nesting of some owl species was noticed in the endmost corner of the Main Chamber. The debris cone under the entrance pit contains up to 3–5 % of bone material, and even more

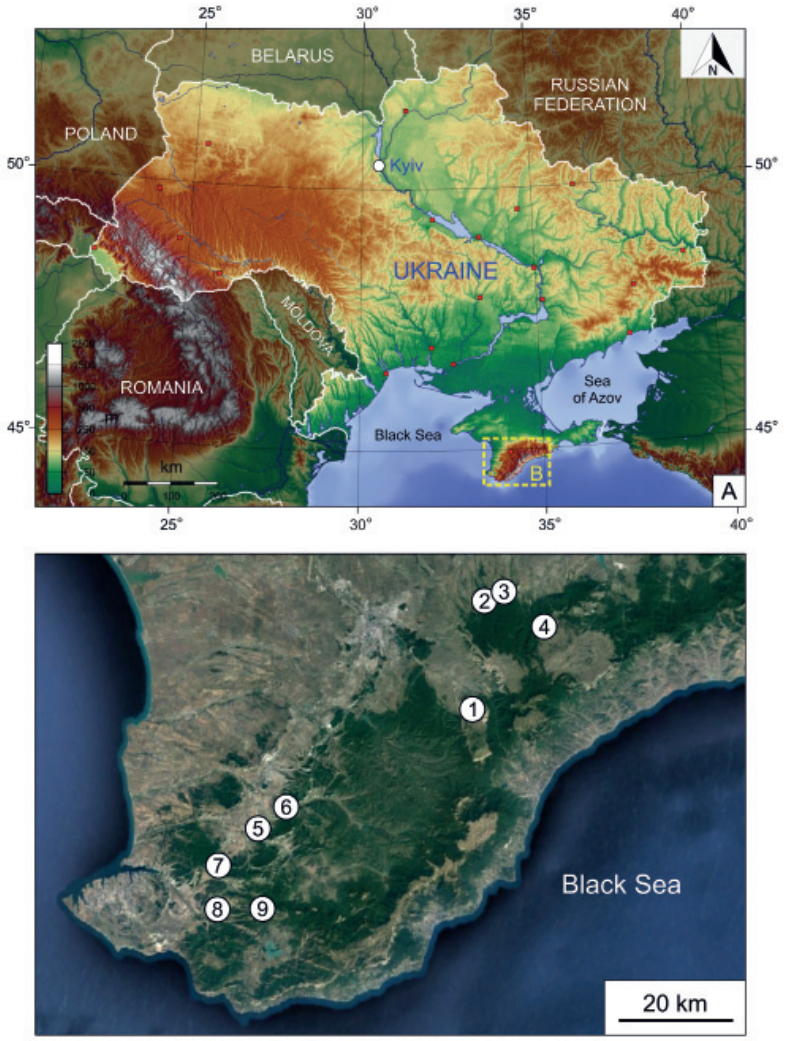

Fig. 1. Map showing the Late Pleistocene and Early Holocene cave sites in the Crimean Peninsula yielding the remains of choughs (*Pyrrhocorax*): 1 — Emine-Bair-Khosar; 2 — Kiik-Koba; 3 — Kosh-Koba; 4 — Adzhi-Koba; 5 — Sjuren 1; 6 — Alymivskyi Navis; 7 — Karani-Koba; 8 — Murzak-Koba; 9 — Fat'ma-Koba.

in the bone-breccia site Bb. The sediments in the cone, consisting mainly of limestone debris, blocks, and loams, gravitationally moved downslope due to the crip process, solifluction. Small particles, including remains of small vertebrates, were also transported by the melt water from snow cone and usually accumulated on the pit bottom during cold and snowy winters (Ridush et al., 2013, 2018).

There are eight bone sites in the cave: Ba1, Ba2, Bb, Bc, Be, Bf, Bg, Bh, and Bj. Only two of them, i. e. Ba2 and Bc, are now well stratified. The Ba2 site contains the following units/layers: A, B, C, D, E, F (Holocene), Unit G (MIS 2), Unit H (MIS 3), and Unit I (MIS 5e, Eemian interglacial) (Bondar & Ridush, 2010; Ridush, 2013; Ridush et al., 2018). The Bc site contains the layers 1, 2a, 2b, 3, 4, and 5 (Vremir & Ridush, 2005). The sequence of cave sediments at the joint section of Ba2 and Bc sites covers the period since the Middle Pleistocene (MIS 7) up to the Late Holocene. The sequence was dated radiometrically during palaeogenetic research of different species, mainly of *Cervus elaphus*, from this site (Stankovic et al., 2011; Gąsiorowski et al., 2014; Doan et al., 2018, 2022; Niedziałkowska et al., 2021). The rest of the sequence was roughly dated using biostratigraphic methods (Ridush et al., 2018). The accumulation of bones occurred there mainly during interglacials (MIS 5e) and interstadials (MIS 3, 5c). The absence of cold-loving faunal elements (e. g. *Rangifer tarandus*) allows us concluding that a snow plug closed the entrance pit during very cold intervals (Ridush et al., 2018).

Kiik-Koba (44°57'54.05" N, 34°21'08.98" E; 515 m a. s. l.; Late Pleistocene). Eight bird bones were found, one of which has been assigned to *P. pyrrhocorax* (Voinstvensky, 1967).

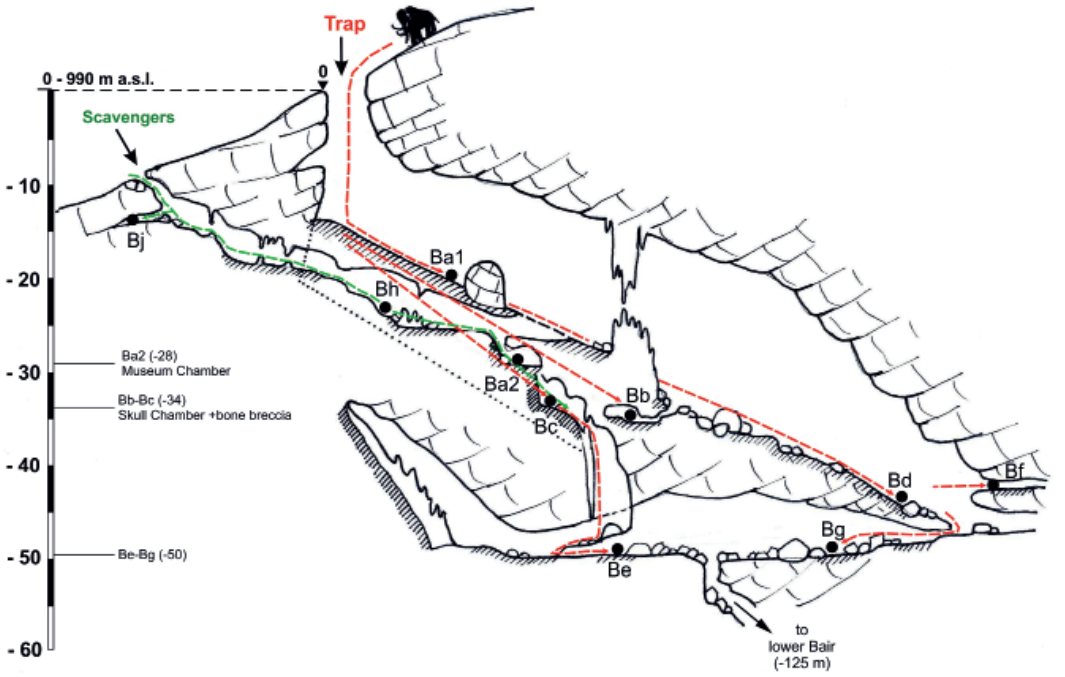

Fig. 2. Locations of bone sites in the Emine-Bair-Khosar Cave on the section (Vremir & Ridush, 2005 modified).

Kosh-Koba (44°58'00.20" N, 34°20'59.99" E; 488 m a. s. l.; Mousterian, Late Pleistocene). Three bird bones were found there, and all referred to as *P. pyrrhocorax* (Voinstvensky, 1967).

Adzhi-Koba (44°54'59.94" N, 34°27'28.04" E; 760 m a. s. l.; Mousterian, Late Pleistocene). A total of 601 bird bones were collected there and now they are deposited in the Zoological Institute (ZISP) of the Russian Academy of Sciences. Of them, six were described as *P. pyrrhocorax* and 29 — as *P. graculus* (Baryshnikov & Potapova, 1988). Another 43 bones are deposited in the NMNHU-P, of which M. Voinstvensky identified six specimens as representing *P. pyrrhocorax* (original labels preserved).

Sjuren 1 (44°39'15.40" N, 33°48'31.90" E; 100 m a. s. l.; Aurignacian–Azilian, Late Pleistocene). Several hundreds of bird bones were found there, their exact number is not known (Voinstvensky, 1967), and most are deposited in ZISP. Of them, 48 bones were identified as belonging to *P. pyrrhocorax* and 126 others — as *P. graculus* (Baryshnikov & Potapova, 1988). Tugarinov (1937) also described the remains from Adzhi-Koba and Sjuren 1 without differentiation by locality. The results of determination of choughs in Tugarinov (1937) differ from those presented in Baryshnikov & Potapova (1988). Other 179 bird bones are deposited at the NMNHU, of which M. Voinstvensky identified two specimens as *P. pyrrhocorax* and three as *P. graculus*. These materials have not been published before.

Alymivskyi Navis (44°41'06.01" N, 33°52'26.07" E; 320 m a. s. l.): 172 bird bones were found, of which six were described as *P. graculus* and one as *Pyrrhocorax* sp. (Voinstvensky, 1967).

Karani-Koba (44°36'07" N, 33°42'57" E; 339 m a. s. l.; Late Palaeolithic, Early Holocene). A total of 114 bird bones were collected on this site; 65 specimens were described as belonging to *P. pyrrhocorax*, and 21 ones — as *P. graculus* (Voinstvensky, 1967). The collection is partially preserved; there are 94 bird bones in the NMNHU-P. Of them, 52 specimens were initially identified by M. Voinstvensky (1967) as *P. pyrrhocorax* (original labels preserved), and seven as *P. graculus*. Another nine bones from the site remain unlabelled; we identified them as belonging to *P. graculus*.

Murzak-Koba (44°31'59.98" N, 33°42'00" E; 156 m a. s. l.). There are 26 bird bones in the material from this site including four specimens identified as *P. graculus* (Voinstvensky, 1967).

Fat'ma-Koba (44°31'55.06" N, 33°48'00.8" E; 437 m a. s. l.; Early Holocene). There are 11 bird bones from this site; one specimen was identified as *P. graculus* (Voinstvensky, 1967).

Results and Comparisons

There are no reliable anatomical differences between bones of extant *Pyrrhocorax pyrrhocorax* and *P. graculus*. In a review of the comparative skeletal anatomy of European corvids (Tomek & Bochenski, 2000), a single difference between these species (the structure of the condylus medialis of the femur) is indicated; the authors pointed the low diagnostic value of this character. Other attempts to find anatomical differences seem to be inconclusive, mainly because different researchers find different discrepancies. For example, Tugarinov (1937) mentioned one difference in the structure of tarsometatarsus (probably referring to the foramen vasculare distale, which in our opinion is a very variable character). He does not specify the number of skeletons in the comparative collection, but it is clear from the text that there were few of them — one *Pyrrhocorax graculus* and a handful of *P. pyrrhocorax*. Jánossy (1974) used the skeletons of three individuals of extant *P. graculus* and two *P. pyrrhocorax*, and indicated anatomical differences in tarsometatarsus, albeit it is difficult to understand which ones. According to his data (Jánossy, 1974), the 'foramina inferiora' are symmetrical in *P. graculus* and asymmetrical in *P. pyrrhocorax*. Probably, the foramen vasculare distale is meant, but this character differs from that suggested by Tugarinov (1937). The latter considered the number of foramina to be a diagnostic character (one in *P. pyrrhocorax* and two in *P. graculus*), while Jánossy (1974) pointed that there are two openings in both species, but they differ in symmetry.

We have examined the available specimens of choughs (eight individuals of *P. graculus* and three individuals of *P. pyrrhocorax*) and do not confirm the reliability of this character. Baryshnikov & Potapova (1988) wrote about the questionable difference in the shape of the processus acrocoracoideus and the depth of the recess in the distal part of carpometacarpus.

Even if the above differences are reliable the authors are limited in its application to distinguish between the two species. Tugarinov (1937) indicated that according to the anatomical differences he discovered all tarsometatarsi belonged to one species, *Pyrrhocorax graculus*. Jánossy (1974) pointed out differences in the structure of tarsometatarsus, but this was one of six fossil chough bones he examined. Baryshnikov & Potapova (1988) tried to exploit the differences in the coracoideum structure, although there were only two coracoidei assigned to *P. graculus* among two hundred bird remains they examined. Fossil remains of the genus *Pyrrhocorax* can only be identified to species level by measurements (Boev & Tsoukala, 2019). It is desirable to use various measurements. Instead, Tugarinov (1937) used a single parameter: the total length. Baryshnikov & Potapova (1988) measured bone length, width of the proximal and distal epiphyses, and the width of the diaphysis.

The total length is a parameter that is often used, but it is not enough to distinguish two species of choughs. In these birds, almost all measurements of tubular bones overlap; the only exception is the total length of humerus, the maximum dimensions of which in *P. graculus* are less than the minimum values of *P. pyrrhocorax* (Tomek & Bochenski, 2000). It is noteworthy that Tugarinov (1937) and Baryshnikov & Potapova (1988) identified all humeri from the Crimea as *P. graculus*. The conclusion that two species of the genus *Pyrrhocorax* differ in the length of wing bones (Jánossy, 1974) was made on a small sample and it was not confirmed using a larger sample (Tomek & Bochenski, 2000). To distinguish the fossil remains, the researcher needs to take a set of measurements on a large sample of extant species.

To our knowledge, no scientific institution has numerous extant *Pyrrhocorax* skeletons. Mourer-Chauviré (1975) combined data from several French scientific institutions;

the total sample in her study included eight individuals of extant *P. pyrrhocorax* and 15 extant individuals of P. *graculus*. Tomek & Bochenski (2000) combined measurements from collections of various institutions in Europe (but not France) and reached a sample of 26 individuals of extant *P. pyrrhocorax* and 49 individuals of extant *P. graculus*.

In the NMNHU-P comparative collection, there are skeletons of three individuals of *P. pyrrhocorax* and six individuals of *P. graculus*. We used them to look for anatomical characters, but did not measure them since Tomek & Bochenski (2000) already used these specimens in the general sample. Their monograph is fundamental for the identification of the *Pyrrhocorax* remains. For some time, it was little known and not referenced in a number of articles published at the beginning of the 21st century (Boev, 2001, 2006 a, b; Mlíkovský, 2009). Now it is used by almost all researchers to identify the fossil remains of the genus *Pyrrhocorax* from Pleistocene localities in Europe (e. g., Rando, 2007; Tomek et al., 2012; Bedetti & Pavia, 2013; Carrera et al., 2018; Suárez-Bilbao et al., 2018; Boev & Tsoukala, 2019).

Baryshnikov & Potapova (1988) used data presented by Mourer-Chauviré (1975), but they had a small comparative collection with a sample from 1–4 individuals (depending on measurement) to 16 individuals (femur). The sample size matters: the mean femur length data in Baryshnikov & Potapova (1988) and Mourer-Chauviré (1975) agree to within 0.01 mm. For other bones, mean values are significantly different, as the difference between samples is sometimes 1 : 14. Under these circumstances, the measurements from Mourer-Chauviré (1975) should be regarded as etalon, and a small sample as an auxiliary one. Instead, the authors consider their small sample as a benchmark (see fig. 7 in Baryshnikov & Potapova, 1988). As a result, they conclude that there was no *Pyrrhocorax graculus vetus* in the Late Pleistocene of the Crimean Peninsula, and the birds should be identified both as *Pyrrhocorax graculus* and *Pyrrhocorax pyrrhocorax*.

If we compare the data on extant birds given by Tugarinov (1937) and Baryshnikov & Potapova (1988) with those on a larger sample (e. g., Tomek & Bochenski, 2000), it is noticeable that previous researchers of fossil birds of the Crimea had a false representation of the difference in size between *P. pyrrhocorax* and *P. graculus*. For example, we will give data on the length of the ulna — this parameter is presented in all sources for both species (table 1), the results for other bones are the same. Tugarinov (1937) underestimated the size of *P. pyrrhocorax* — the maximum size presented by him is only slightly larger than the average in a large sample. Baryshnikov & Potapova (1988), on the contrary, overestimated the sizes: the minimum value in their sample is closer to the average in a large sample. This probably led to large discrepancies in the results. Tugarinov (1937) identified even small birds as *Pyrrhocorax pyrrhocorax*, while Baryshnikov & Potapova (1988) assigned only large individuals to this species. Therefore, according to Tugarinov (1937), the ratio

Table 1. Comparison of data on the length of ulna in extant *Pyrrhocorax pyrrhocorax* and *P. graculus*

Species	n	Length of the ulna, mm			References
		minimum	maximum	mean	
P. pyrrhocorax	?	58.1	67.6	–	Tugarinov, 1937
	6	63.2	72.6	66.6	Baryshnikov & Potapova, 1988
	22	56.0	72.5	65.2	Tomek & Bochenski, 2000
P. graculus	1	56.3	–	–	Tugarinov, 1937
	2	56.3	56.5	–	Baryshnikov & Potapova, 1988
	31	54.2	62.0	57.4	Tomek & Bochenski, 2000

of the *P. pyrrhocorax* to *P. graculus* remains is close to 1 : 1, however this proportion is 1 : 3 in the Adzhi-Koba and Sjuren 1 according to Baryshnikov & Potapova (1988). In total, they determined the same 209 specimens of the genus *Pyrrhocorax*, but the discrepancy in results is very significant with such a sample size. Voinstvensky (1967) did not specify by which characters he distinguished the two chough species. His work is a survey of fossil birds of Ukraine from the Miocene up to the Holocene, and birds of the genus *Pyrrhocorax* are mentioned together with dozens of other species from the Late Pleistocene of the Crimea. However, there are bones he examined and his labels in the NMNHU. We checked the definitions in each case. M. Voinstvensky doubted the accuracy of the identification (species names on the labels crossed out and written again). Sometimes he identified the remains to a species level even if bones are poorly preserved and it is impossible to take any measurements. According to our data, 13 specimens of 65 bones from the Kara-Koba Cave, which Voinstvensky (1967) identified as *Pyrrhocorax pyrrhocorax*, are not suitable for measurements, so it is impossible to establish the species properly. The same applies to five bones (out of 10) from Kosh-Koba, three bones (out of five) from the Adzhi-Koba Cave, and two bones (out of 4) from the Murzak-Koba Cave.

Table 2. Measurements of bones from the Late Pleistocene of the Crimea identified as *Pyrrhocorax pyrrhocorax* by Voinstvensky (1967)* and their comparison with those in extant *Pyrrhocorax*

Bone	Locality, inventory number	Measurements, mm		
		total length	proximal width	distal width
Humerus	Kosh-Koba, NMNHU-P Av-7078	–	–	13.2
	Karani-Koba, NMNHU-P Av-10729	–	13.2	–
	Karani-Koba, NMNHU-P Av-10741	–	13.6	–
	Karani-Koba, NMNHU-P Av-10760	43.2	13.5	11.7
	Karani-Koba, NMNHU-P Av-10761	46.4	15.6	13.2
	extant *P. graculus* (minimum)**	40.6	13.2	10.5
	extant *P. graculus* (maximum)**	46.0	15.7	12.6
	extant *P. pyrrhocorax* (minimum)**	48.4	13.7	11.0
	extant *P. pyrrhocorax* (maximum)**	58.7	17.6	13.6
	extant *P. pyrrhocorax* (mean)**	52.9	15.7	12.5
Carpometacarpus	Karani-Koba, NMNHU-P Av-10745	36.0	9.5	9.1
	Karani-Koba, NMNHU-P Av-10816	37.4	9.2	–
	Murzak-Koba, NMNHU-P Av-10831	36.6	–	9.4
	extant *P. graculus* (minimum)**	33.5	7.8	7.4
	extant *P. graculus* (maximum)**	38.1	9.0	8.9
	extant *P. pyrrhocorax* (minimum)**	35.8	8.0	8.2
	extant *P. pyrrhocorax* (maximum)**	43.3	10.2	10.0
	extant *P. pyrrhocorax* (mean)**	38.9	9.2	9.0
Tarsometatarsus	Karani-Koba, NMNHU-P Av-10736	–	7.4	–
	Karani-Koba, NMNHU-P Av-10759	46.2	7.1	5.1
	Karani-Koba, NMNHU-P Av-10784	–	7.3	–
	Karani-Koba, NMNHU-P Av-10807	–	7.7	–
	extant *P. graculus* (minimum)**	41.8	6.6	4.7
	extant *P. graculus* (maximum)**	48.9	7.8	5.7
	extant *P. pyrrhocorax* (minimum)**	45.9	7.3	4.9
	extant *P. pyrrhocorax* (maximum)**	56.4	8.6	6.4
	extant *P. pyrrhocorax* (mean)**	51.0	7.9	5.5

*The table does not show the results of measurements of ulnae (20 specimens), radii (3 specimens), femori (7 specimens), and tibiotarsi (8 specimens). All these bones are damaged and it is impossible to measure their total length. The results of other measurements corroborate the general conclusion.

**Data after Tomek & Bochenski (2000).

The identification of bones that are suitable for measurements is questionable. The remains identified by Voinstvensky (1967) as *Pyrrhocorax pyrrhocorax* are small as for this species (table 2). Their diameters in most cases are within the range characteristic of *P. graculus*. In some cases, the size of bones is larger than that of extant *P. graculus*, but not more than 0.2–0.5 mm. All fossil bones are smaller than or close to the average size of those in extant *P. pyrrhocorax*. If we accept Voinstvensky's conclusion that these remains represent *P. pyrrhocorax*, the question arises why all of them are so small. There is no question if we accept that there was no *P. pyrrhocorax* in the Late Pleistocene of the Crimea, and all the bones belong to *P. graculus*.

The femur NMNHU Av-2128 from Adzhi-Koba was misidentified by Voinstvensky as *P. pyrrhocorax*. In fact, it belongs to a rook *Corvus frugilegus*. This is evidenced by the measurements — the total length is 46.5 mm, while the maximum length of *P. pyrrhocorax* is 46.0 mm (Tomek & Bochenski, 2000). The bone is also distinguished by an edge of the facies articularis antitrochanterica (cranial view) and a rounded crista tibiofibularis (lateral view), which is not characteristic for *Pyrrhocorax*.

Considering the above, we believe that the identification of bird remains from the Late Pleistocene of the Crimean Peninsula as *P. pyrrhocorax* does not have sufficient arguments. By all measurements, these remains correspond to or are very close to those in extant *P. graculus*. Minor deviations allow us to assume that the remains belonged to an extinct subspecies.

To clarify this question, we investigate bird remains from the Emine-Bair-Khosar Cave — the locality with the largest number of chough bones in the Crimea. Among 722 bones belonging to *Pyrrhocorax*, 630 were found in layers dated to the Late Pleistocene, 19 — to the Early Holocene, and 73 specimens come from layers lacking precise dating. The bones of Pleistocene age were used for the identification of the subspecies, while the remains of the other age were used as additional ones when checking anatomical characters and clarifying the ecological niche. The total length of tubular bones (number of identifiable specimens — 108) revealed that birds of the genus *Pyrrhocorax* from the Late Pleistocene of the Crimea were smaller than extant *P. pyrrhocorax* (fig. 3). The maximum size of the bones is smaller than the mean for *P. pyrrhocorax*, and the maximum size of humeri is smaller than the minimum for *P. pyrrhocorax*.

Birds from the Late Pleistocene of the Crimea belonged to the same size class as extant *P. graculus*, although some differences in the total length of tubular bones are also noticeable. Comparison of two samples using Student's t-test revealed significant differences in size between the fossil *Pyrrhocorax graculus* from Emine-Bair-Khosar and extant *P. graculus* (tables 3–9, fig. 3). No differences were found for ulnae (radii were not used as they are represented only by two specimens). Most of the differences are in carpometacarpi. *Pyrrhocorax* from Emine-Bair-Khosar was distinguished by a shorter length of carpometacarpus, a smaller width of its proximal and distal ends, and a smaller width of the distal part of os metacarpale minus. Fossil specimens have a narrower proximal end of humerus, but a greater depth of the caput humeri. The distal end of the humerus was wider. Fossil specimens also had a larger diaphysis of coracoid, tibiotarsus, and tarsometatarsus.

The subspecies *Pyrrhocorax graculus vetus* from the type locality of Saint-Estève, France (Middle Pleistocene) differs from the extant species in all the indicated characters (Mourer-Chauviré, 1975; measurements of the width of the distal part of os metacarpale minus and the depth of the caput humeri are not given in the original description). The only noticeable difference between the birds from the Crimea and *Pyrrhocorax graculus vetus* is the length of tibiotarsus. In birds from the type locality, the mean value is 69.6 mm, while it equals

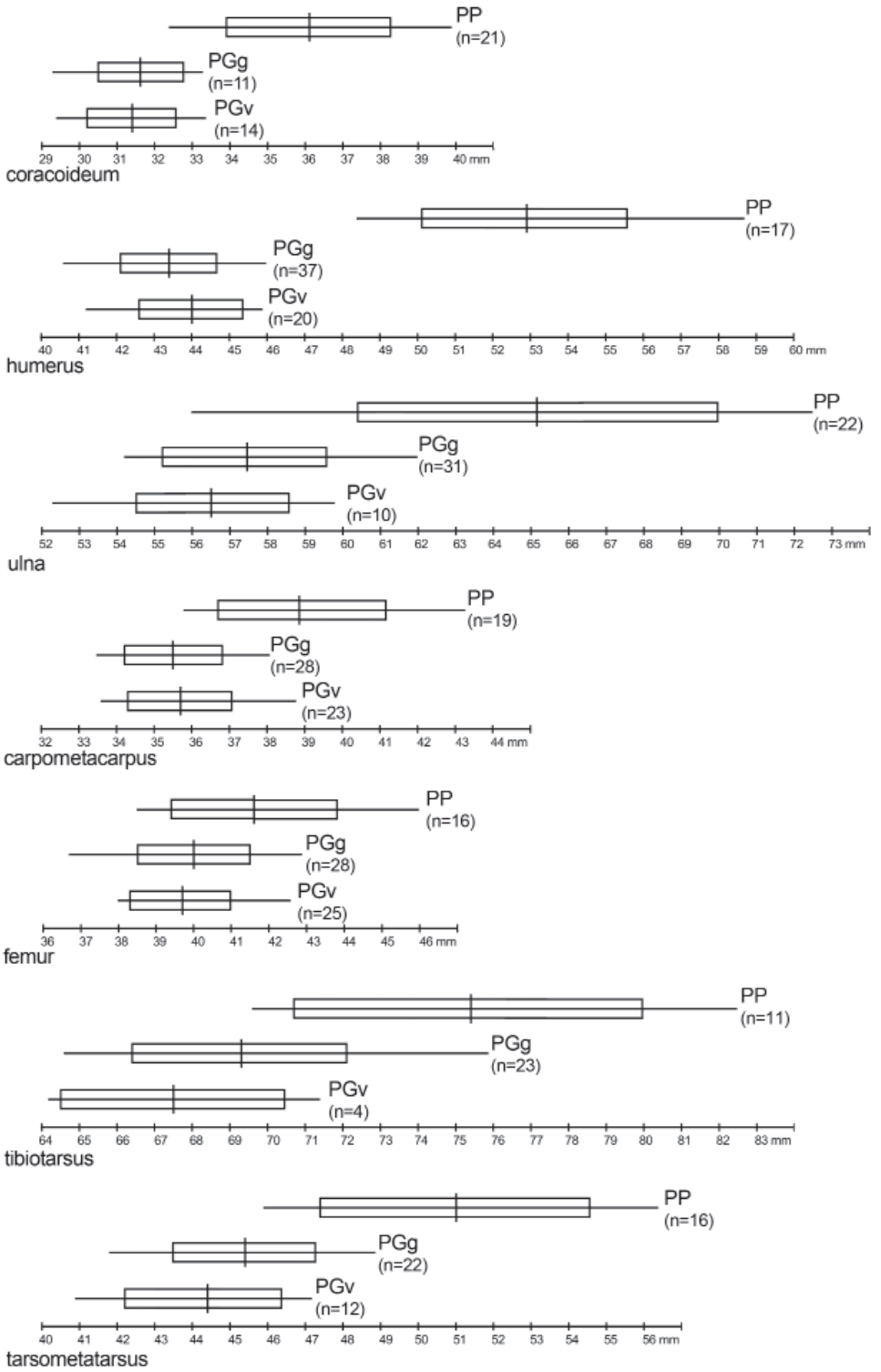

Fig. 3. Minimal and maximal values, arithmetic mean and standard deviation (SD) for the total length of coracoideum, humerus, ulna, carpometacarpus, femur, tibiotarsus and tarsometatarsus: PP — extant *Pyrrhocorax pyrrhocorax* (after Tomek & Bochenski, 2000); PGg — extant *Pyrrhocorax graculus graculus* (after Tomek & Bochenski, 2000); PGv — *Pyrrhocorax graculus vetus* from the Emine-Bair-Khosar Cave (our data); n — number of specimens.

to 67.5 mm in individuals from the Crimea. However, both values fall into the range characteristic of extant *Pyrrhocorax graculus*: 64.5–75.2 mm (Tomek & Bochenski, 2000), and the discrepancy may be due to a small sample size (there are hundreds of bones in the type locality, but only five tibiotarsi suitable for measurements, instead four complete tibiotarsi, were found in Emine-Bair-Khosar). In the original description of *Pyrrhocorax graculus vetus* (Mourer-Chauviré, 1975), it is noted that some bones are slightly shorter than those in extant *Pyrrhocorax graculus* but more massive. This characteristic also applies to choughs from the Emine-Bair-Khosar. Bird remains from the Middle Pleistocene of France and Late Pleistocene of the Crimea are similar in how they differ from extant birds in terms of total length (fig. 4). If it were a coincidence, the difference would be proportional to the length

Table 3. Comparison of measurements (in mm) of coracoidei of *Pyrrhocorax graculus vetus* from Emine-Bair-Khosar and extant *Pyrrhocorax graculus* (after Tomek & Bochenski, 2000)

Measurements	Extinct *P. graculus vetus*			Extant *P. graculus*			t practical	t critical	Statistically significant difference (yes/no)
	n	mean	SD	n	mean	SD			
Total length	14	31.4	1.2	21	31.6	1.2	0.48	2.04	no
Medial length	16	29.5	1.1	22	29.4	1.1	0.28	2.03	no
Minimum diameter of the shaft	17	2.5	0.2	24	2.3	0.2	3.15	2.02	yes
Sternal width	14	9.0	0.4	21	9.0	0.6	0	2.02	no
Depth of the sternal part	16	2.9	0.3	25	2.7	0.2	2.57	2.02	yes

Table 4. Comparison of measurements (in mm) of humeri of *Pyrrhocorax graculus vetus* from Emine-Bair-Khosar and extant *Pyrrhocorax graculus* (after Tomek & Bochenski, 2000)

Measurements	Extinct *P. graculus vetus*			Extant *P. graculus*			t practical	t critical	Statistically significant difference (yes/no)
	n	mean	SD	n	mean	SD			
Total length	20	44.0	1.4	37	43.4	1.3	1.62	2.00	no
Proximal width	18	13.8	0.7	32	14.2	0.6	2.13	2.01	yes
Distal width	25	11.8	0.5	37	11.3	0.4	4.36	2.00	yes
Depth of the condylus dorsalis	23	5.8	0.4	39	5.5	0.2	3.94	2.00	yes
Maximum diameter of the shaft	26	4.7	0.4	40	4.6	0.2	1.35	2.00	no
Height of the processus supracondylaris dorsalis	21	6.3	0.4	32	6.4	0.3	1.03	2.01	no
Minimum diameter of the shaft	26	3.8	0.2	40	3.7	0.2	1.98	2.00	no

Table 5. Comparison of measurements (in mm) of ulnae of *Pyrrhocorax graculus vetus* from Emine-Bair-Khosar and extant *Pyrrhocorax graculus* (after Tomek & Bochenski, 2000)

Measurements	Extinct *P. graculus vetus*			Extant *P. graculus*			t practical	t critical	Statistically significant difference (yes/no)
	n	mean	SD	n	mean	SD			
Total length	10	56.5	2.1	31	57.4	2.2	1.14	2.02	no
Proximal width	15	7.8	0.4	34	7.6	0.4	1.61	2.01	no
Proximal height	15	8.4	0.5	31	8.5	0.4	0.73	2.02	no
Height of the processus cotylaris dorsalis	10	3.7	0.3	32	3.6	0.3	0.92	2.02	no
Minimum diameter of the shaft	16	3.7	0.2	38	3.6	0.3	1.22	2.01	no
Diagonal distal width	14	7.4	0.3	41	7.3	0.3	1.08	2.01	no
Depth of the condylus dorsalis	14	4.8	0.3	37	4.7	0.4	0.85	2.01	no

Table 6. Comparison of measurements (in mm) of carpometacarpi of *Pyrrhocorax graculus vetus* from Emine-Bair-Khosar and extant *Pyrrhocorax graculus* (after Tomek & Bochenski, 2000)

Measurements	Extinct *P. graculus vetus*			Extant *P. graculus*			t practical	t critical	Statistically significant difference (yes/no)
	n	mean	SD	n	mean	SD			
Total length	23	34.2	1.4	28	35.5	1.3	3.43	2.01	yes
Proximal width	31	8.1	0.4	29	8.4	0.3	3.27	2.00	yes
Proximal height	31	6.1	0.5	29	6.5	0.3	3.72	2.00	yes
Cranial length	26	31.1	1.2	29	32.0	1.1	2.9	2.01	yes
Length of the os metacarpale alulare	27	4.1	0.2	29	4.1	0.2	0	2.01	no
Depth of the trochlea carpalis, measured with the processus pisiformis	23	5.1	0.3	27	5.3	0.4	1.97	2.01	no
Maximum distal width	24	7.9	0.6	25	8.1	0.4	1.38	2.01	no
Maximum width of the distal part of the os metacarpale minus	25	4.1	0.3	25	4.4	0.2	4.16	2.01	nes

Table 7. Comparison of measurements (in mm) of femori of *Pyrrhocorax graculus vetus* from Emine-Bair-Khosar and extant *Pyrrhocorax graculus* (after Tomek & Bochenski, 2000)

Measurements	Extinct *P. graculus vetus*			Extant *P. graculus*			t practical	t critical	Statistically significant difference (yes/no)
	n	mean	SD	n	mean	SD			
Total length	25	39.7	1.3	28	40.0	1.5	0.77	2.01	no
Proximal width	32	7.2	0.4	30	7.3	0.2	1.23	2.00	no
Minimum diameter of the shaft, measured at the middle of its length	33	3.1	0.3	26	3.0	0.1	1.62	2.00	no
Distal width	27	7.6	0.3	27	7.7	0.3	1.22	2.01	no
Depth of the condylus medialis, measured with the long axis of the bone parallel to the calipers	26	4.3	0.2	25	4.5	0.3	2.81	2.01	yes
Depth of the tibial part of the condylus lateralis	27	5.9	0.2	27	6.1	0.3	2.88	2.01	yes
Depth of the fibular part of the condylus lateralis	27	4.8	0.3	23	5.0	0.2	2.7	2.01	yes

Table 8. Comparison of measurements (in mm) of tibiotarsi of *Pyrrhocorax graculus vetus* from Emine-Bair-Khosar and extant *Pyrrhocorax graculus* (after Tomek & Bochenski, 2000)

Measurements	Extinct *P. graculus vetus*			Extant *P. graculus*			t practical	t critical	Statistically significant difference (yes/no)
	n	mean	SD	n	mean	SD			
Total length	4	67.5	3.0	23	69.3	2.9	1.14	2.06	no
Proximal width I: distance between the facies articularis medialis and the facies articularis lateralis	9	6.5	0.3	28	6.5	0.3	0	2.03	no
Proximal width II: distance between the facies articularis medialis and crista cnemialis lateralis	7	9.7	0.4	21	9.7	0.3	0	2.06	no
Distal width	17	6.1	0.3	30	6.1	0.2	0	2.01	no
Depth of the condylus distalis medialis	16	5.9	0.2	28	6.1	0.3	2.38	2.02	yes
Minimum diameter of the shaft	15	3.0	0.1	31	2.8	0.2	3.64	2.02	yes

Table 9. Comparison of measurements (in mm) of tarsometatarsi of *Pyrrhocorax graculus vetus* from Emine-Bair-Khosar and extant *Pyrrhocorax graculus* (after Tomek & Bochenski, 2000)

Measurements	Extinct *P. graculus vetus*			Extant *P. graculus*			t practical	t critical	Statistically significant difference (yes/no)
	n	mean	SD	n	mean	SD			
Total length	12	44.3	2.1	22	45.4	1.9	1.56	2.04	no
Proximal width	13	7.0	0.4	25	7.1	0.3	0.87	2.03	no
Distal width	21	5.2	0.3	22	5.2	0.2	0	2.02	no
Minimum diameter of the shaft	21	2.9	0.2	24	2.6	0.1	6.48	2.02	yes

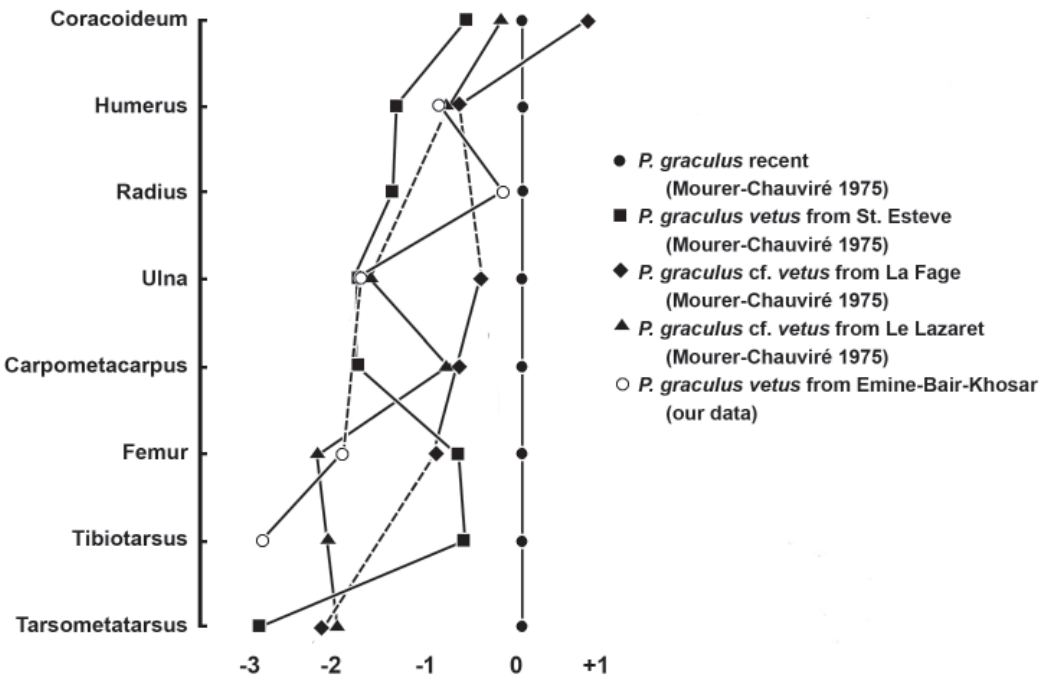

Fig. 4. Differences in the length of tubular bones of *Pyrrhocorax graculus vetus* and extant *Pyrrhocorax graculus*. Data on the remains from France and extant birds follow Mourer-Chauviré (1975). Measurements are presented according to the scheme in Mourer-Chauviré (1975).

of the skeletal element; however, such a regularity is not noticeable. The biggest difference is in the length of tarsometatarsi and carpometacarpi, while the difference between the ulnae (one of the longest bones in the avian skeleton) is much smaller. Since the birds from the Emine-Bair-Khosar differ from extant *Pyrrhocorax graculus* and do not differ from *Pyrrhocorax graculus vetus* Mourer-Chauviré 1975, we believe that the population of this subspecies existed in the Late Pleistocene of the Crimea.

In the original description of this subspecies, it is indicated that it differs from the extant species only in measurements while there are no anatomical differences. Based on the finds from the Crimea, some characters were found in the place of the shoulder joint of *Pyrrhocorax graculus vetus*. They differ from the extant species by a better developed attachment point for the musculus pectoralis on humerus. The impressio musculus pectoralis in the place of transition into crista deltopectoralis has a clear edge; crista deltopectoralis has a concavity in the proximal edge. The pneumatic opening on the tuberculum brachiale of

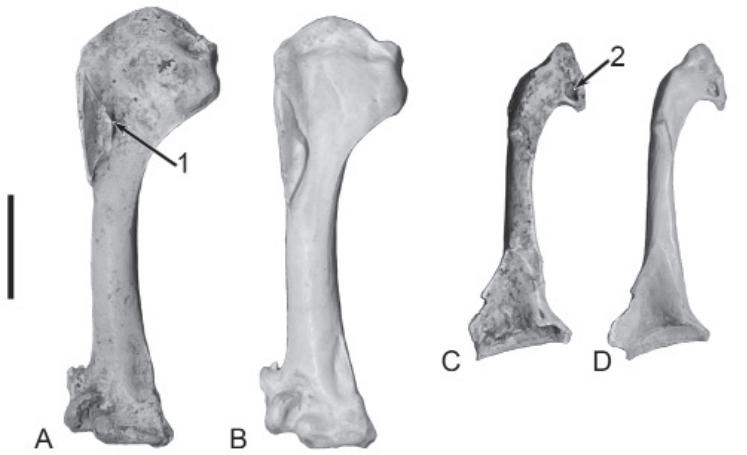

Fig. 5. Humerus (A) and coracoideum (C) of *Pyrrhocorax graculus vetus* from Emine-Bair-Khosar compared to respective bones (B, D) of *Pyrrhocorax graculus*. Arrows indicate a clear edge of the impressio musculus pectoralis (1) and a large tuberculum brachiale (2).

the coracoideum is larger as compared to that in extant *Pyrrhocorax* (88%, n = 16) (fig. 5). These characters may reflect individual variability; it is difficult to use them in subspecies diagnostics.

Discussion

During the Late Pleistocene, the Alpine chough *Pyrrhocorax graculus* was widely distributed in the mountainous regions of Europe, from the Atlantic islands in the west to the Caucasus in the east (Boev, 1999). At the same time, the subspecies *Pyrrhocorax graculus vetus* was recorded only from Eastern Europe between 24° and 16° E longitude — in the Devetashka Cave, Bulgaria (Boev, 1999), Treugolnaya Cave, North Caucasus (Potapova & Baryshnikov, 1993), and Emine-Bair-Khosar in Ukraine (our data). In Western Europe,

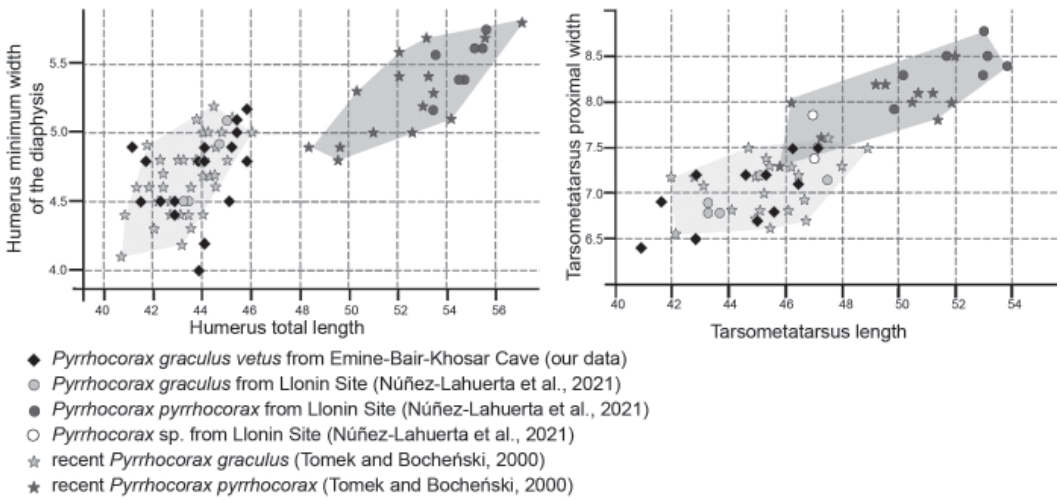

Fig. 6. Measurements of humerus (A) and tarsometatarsus (B) of *Pyrrhocorax graculus vetus* from the Emine-Bair-Khosar Cave (Late Pleistocene, Ukraine), *Pyrrhocorax graculus* from Llonin Cave (Late Pleistocene, Spain) and extant *Pyrrhocorax graculus*.

Pyrrhocorax graculus (without specifying the subspecies) is mentioned, although localities of Late Pleistocene age with a large number of its remains are known for this territory. Even the author of the original description of the subspecies identified 82 bones from the Grotte du bois du Canet (France) simply as *Pyrrhocorax graculus* (Clot et al., 1984). At Llonin Cave (Spain), 27 remains of *Pyrrhocorax graculus* were found, all with diameters in the range typical for the extant *Pyrrhocorax graculus* (Núñez-Lahuerta et al., 2021). Comparison of the measurements from Spain and Emine-Bair-Khosar indicates a difference: in the Late Pleistocene of Spain there were birds that do not differ from extant ones, while in the Late Pleistocene of the Crimea there were birds that differ both from extant ones and those from Spain (fig. 6). This allows us to assume that the range of *Pyrrhocorax graculus vetus* in Europe was reduced during the Late Pleistocene, and this subspecies occurred only in the north of the Balkan Mountains, in the Crimean Mountains and the North Caucasus. In Pleistocene layers of the Emine-Bair-Khosar Cave, the bones of *Pyrrhocorax graculus* constitute 96.8 % of all bird remains. The relative abundance of this species on the site during the Early Holocene is less than 20 % (table 10), in later times, choughs were not observed in the Crimea at all (Kostin, 2006). Apparently, warming has changed local ecosystems and these birds have disappeared. Nowadays, *Pyrrhocorax graculus* (fig. 7) occurs in mountainous areas of Europe at 1500–3000 m a. s. l.

Fig. 7. Alpine chough *Pyrrhocorax graculus*. Drawing by Velizar Simeonovski.

Table 10. Percentage of bird species in layers of Late Pleistocene and Early Holocene age of the Emine-Bair-Khosar Cave

Species	Late Pleistocene (NISP* 651)	Early Holocene (NISP* 95)
Pyrrhocorax graculus vetus	96.8	20.0
Turdus merula	0	2.1
Sylvia atricapilla	0	4.2
Galerida cristata	0.2	0
Alauda arvensis	0	3.2
Anthus spinoletta	0	1.1
Passer sp.	0.2	0
Phylloscopus collybita/trochilus	0.2	0
Caprimulgus europaeus	0.3	0
Jynx torquilla	0	1.1
Lagopus lagopus	0	1.1
Coturnix coturnix	0	5.3
Columba livia/oenas	2.2	55.8
Falco tinnunculus	0.2	0
Gallinago media	0.2	0

*NISP — number of identifiable specimens.

(Cramp & Perrins, 1994), while the highest peak of the Crimean Mountains is 1545 meters. It means that there are no ecosystems suitable for the existence of *Pyrrhocorax graculus* in the Crimea in modern climatic conditions. The range of *Pyrrhocorax graculus* also decreased due to warming in other regions of Europe during Holocene (Carrera et al., 2022).

The identification of the subspecies and its discovery in the Crimea is a new puzzle to the natural history of *Pyrrhocorax graculus*. Much more important is the conclusion that only one chough species (not two) have occurred in this region during the Pleistocene. Findings of its remains are indicators of past climatic conditions. For example, in a review devoted to a relict fauna of the Ice Age, Tyrberg (1991, p. 38) stated that 'the differences in the Würmian ranges of the two *Pyrrhocorax* species may be due to a greater tolerance for cold continental climates by the Alpine Chough'. We agree with this conclusion of Tyrberg (1991) but note one inaccuracy. The review states that two species of the genus *Pyrrhocorax* coexisted in western and southern regions of Europe, as well as in the Crimea, whereas *P. graculus*, adapted to cold conditions, was more numerous in Eastern Europe (Tyrberg, 1991). If we accept that *P. pyrrhocorax* was absent in the Crimea during the Late Pleistocene, this even strengthens the above statement.

The results obtained indicate cold conditions in the Crimea during the Late Pleistocene. The climate was even colder than that in other regions of Europe located at the same latitude (44° N). The species composition of birds in each Late Pleistocene locality in Europe is different, but there are common features. There are birds representing various ecological niches, in particular open landscapes, forest steppes and forests. Indicators of open landscapes in materials from the Late Pleistocene localities are ptarmigans (*Lagopus lagopus*, *L. muta*) and phasianids (*Perdix perdix*, *P. paleoperdix*, *Coturnix coturnix*, *Alectoris* sp.). The presence of trees is indicated by the findings of grouses (*Tetrao urogallus*, *Lyrurus tetrix*, *Bonasia bonasia*), thrushes (*Turdus merula*, *T. philomelos*, *T. iliacus*, *T. pilaris*, *T. viscivorus*), and woodpeckers (*Picus viridis*, *Dendrocopos major*, *D. medius*, *Dryobates minor*). This group also includes pigeons, which have a great ecological plasticity, but in the wild prefer forested areas (Murton & Westwood, 1966).

Temperatures in the mountainous regions of Europe, at least during nesting season, were not low, there were many insects, and there are numerous remains of birds that catch insects on the fly, in particular swallows (*Delichon urbicum*, *Hirundo rustica*, *Cecropis daurica*, *Riparia riparia*, *Ptyonoprogne rupestris*) and swifts (*Tachymarptis melba*, *Apus apus*, *A. pallidus*) in large samples. The red-billed chough *Pyrrhocorax pyrrhocorax* catches insects on the ground surface. If the diet of *Pyrrhocorax graculus* includes insects only during warm months, they are the main food for *P. pyrrhocorax* throughout the year (Laiolo & Rolando, 1999). In addition, there should have been numerous rodents in palaeoecosystems, and therefore the remains of birds of prey were also found, including owls (*Surnia ulula*, *Asio flammeus*, *A. otus*, *Aegolius funereus*, *Atene noctua*, *Strix aluco*, *S. uralensis*, *Bubo scandiacus*) and falcons (*Falco tinnunculus*, *F. vespertinus*). A variety of conditions and not extremely low temperatures attract crows (*Corvus corone* / *frugilegus*, *C. monedula*, *C. corax*). All the groups of birds listed are present in Pleistocene localities of Europe, in which choughs have been found. An exception is the Emine-Bair-Khosar (table 11). More than 96 % of a large sample (651 bird bones) from this site are represented by a single species — *P. graculus*. It allows us to assume extreme climatic conditions in this region as evidenced by the absence of dendrophylous species (except for a small number of pigeons that prefer ecosystems with trees but can also inhabit rocky areas) as well as migratory species arriving during warm season.

Table 11. Representation (in %) of birds of particular ecological groups in the Late Pleistocene of Europe

Species or species group**	Locality									
	West ←								→ East	
	LC*	AR*	SC*	GC*	BH*	BC*	FC*	KZ*	TC*	EB*
P. graculus	48.1	41.7	1.9	42.2	3.1		16.7	3.9	3.8	96.8
P. pyrrhocorax	11.1	22.2	3.2	4.2	0.8		4.2	2.6	0	0
Lagopus sp.	7.4	0	2.3	0.6	0.8		4.2	2.6	0	0
Phasianidae of temperate open landscape	0	8.3	1.4	3.0	2.3		8.3	36.4	26.9	0
Grouses	3.7	11.1	1.9	4.2	21.9		8.3	13.0	3.8	0
Woodpeckers	0	0	0	0	0.8		0	0	3.8	0
Thrushes	11.1	0	1.9	6.0	3.9		0	2.6	3.8	0
Pigeons	3.7	0	2.4	13.3	0		0	0	0	2.2
Owls	0	0	3.2	0.6	6.3		4.2	0	11.5	0
Falcons	0	0	0.9	2.4	3.9		4.2	5.2	11.6	0.2
Swifts	0	0	0.5	0.6	3.1		0	0	3.8	0
Swallows	0	0	0.5	3.6	3.2		4.2	3.9	0	0
Crows	3.7	8.3	2.4	0.6	2.4		3.9	4.2	19.2	0

*LC — Llonin Cave, layer C-VIII, Spain (Núñez-Lahuerta et al., 2021); AR — Artazu VII, Lower Ledge, Spain (Suárez-Bilbao et al., 2018); SC — Santa Catalina Cave, Spain (Marco et al., 2018); GC — Grotte du bois du Canet, France (Clot et al., 1984); BH — Berici Hills, Italy (Carrera et al., 2018); BC — Biśnik Cave, Complex VI, Poland (Tomek et al., 2012); FC — Filipovska Cave, Bulgaria (Boev, 2001); KZ — Kozarnika, Bulgaria (Boev, 2001); TC — Temnata Cave, layer 3a, Bulgaria (Boev, 1994); EB — Emine-Bair-Khosar Cave, Crimea, Ukraine (our data). **Scientific names of species are presented in the text.

Further palaeontological investigations in the Crimea together with a thorough revision of previously published data are important for the study of animal assemblages and estimating palaeoecological changes in this region during the Late Pleistocene and Holocene.

Acknowledgements

The research of LG and OK was carried out in framework of the scientific topic 0120U100451 (National Museum of Natural History of the National Academy of Sciences of Ukraine). We are grateful to late M. Voinstvensky (1916–1996) for the establishment of a comparative osteological collection in the NMNHU and collecting some of the finds discussed herein. We are indebted to Z. Bochenski (Institute of Systematics and Evolution of Animals of the Polish Academy of Sciences) and Z. Boev (National Museum of Natural History of the Bulgarian Academy of Sciences) for their constructive reviews of the manuscript. We further wish to thank V. Simeonovski (Field Museum of Natural History, Chicago, USA) for the Alpine chough drawing.

References

Baryshnikov, G. & Potapova, O. 1988. Middle Palaeolithic birds of the Crimea. *Proceedings of the Zoological Institute of the Academy of Sciences of USSR*, **182**, 40–64 [In Russian].

Baryshnikov, G. & Potapova, O. 1992. Palaeolithic birds of the Crimean Peninsula, USSR. *Natural History Museum of Los Angeles County Scientific Series*, **36**, 293–305.

Baryshnikov, G. F. & Potapova, O. R. 1995. Pleistocene birds from the Acheulean site of the Treugolnaya Cave in the northern Caucasus. *Courier Forschungsinstitut Senckenberg*, **181**, 241–248.

Baumel, J. J., King, A. S., Breazile, J. E., Evans, H. E. & Vanden Berge, J. C., eds. 1993. *Handbook of Avian Anatomy: Nomina Anatomica Avium*. 2nd Edition. Publications of the Nuttall Ornithological Club, No. 23. Nuttall Ornithological Club, Cambridge-Massachusetts, i-xxiv+779+Tab. 1–2.

Bedetti, C. & Pavia, M. 2013. Early Pleistocene birds from Pirro Nord (Puglia, southern Italy). *Palaeontographica Abteilung A*, **298** (1–6), 31–53.

Best, J., Doherty, S., Armit, I., Boev, Z., Büster, L., Cunliffe, B., Foster, A., Frimet, B., Hamilton-Dyer, S., Higham, T., Lebrasseur, O., Miller, H., Peters, J., Seigle, M., Skelton, C., Symmons, R., Thomas, R., Trentacoste, A., Maltby, M., Larson, G. & Sykes, N. 2022. Redefining the timing and circumstances of the chicken's introduction to Europe and north-west Africa. *Antiquity*, **96** (388), 868–882. https://doi.org/10.15184/aqy.2021.90

Boev, Z. 1994. The Upper Pleistocene Birds. *In*: Kozlowski, J. K., Laville, H. & Ginter, B., eds. *Temnata Cave. Excavations in Karlukovo Karst Area, Bulgaria*. Jagellonian University Press, Cracow, 55–86.

Boev, Z. 1999. *Neogene and Quaternary birds (Aves) from Bulgaria*. D. Sci. thesis, National Museum of Natural History, Bulgarian Academy of Sciences, Sofia, 1–135+Tab. 1–251 [In Bulgarian].

Boev, Z. 2000. Late Pleistocene Avifauna of the Razhishkata Cave, Western Bulgaria. *Historia naturalis bulgarica*, **12**, 71–87.

Boev, Z. 2001. Late Pleistocene and Holocene avifauna from three caves in the vicinity of Tran (Pernik District —W Bulgaria). *In*: Delchev, P., Shanov, S. & Benderev, A., eds. *Karst. Vol. I., Proceedings of the First National Conference on Environment and Cultural Heritage in Karst. Sofia, 10–11 November 2000*. Earth and Man National Museum, Association of Environment and Cultural Heritage in Karst, Sofia, 98–106.

Boev, Z. 2006 a. Early Pleistocene avifauna of Kunino (NW Bulgaria). *Historia naturalis bulgarica*, **17**, 125–132.

Boev, Z. 2006 b. Middle Pleistocene birds from the Morovitsa Cave (Lovech District, NC Bulgaria). *In*: *Proceedings of the jubilee scientific conference "75 years of organised speleology in Bulgaria"*. Sofia, 103–110.

Boev, Z. & Tsoukala, E. 2019. Late Pleistocene and Earliest Holocene avifauna from the Loutra Almopias Cave (Macedonia, Greece). *Historia naturalis bulgarica*, **40**, 1–31.

Bondar, K. & Ridush, B. 2010. The dynamics of climate change in Crimea in Holocene-Late Pleistocene after magnetic research of sediments in the Emine-Bair-Khosar Cave. *Visnyk Kyivskoho Universytetu (Geologiya)*, **48**, 39–44.

Čapek, V. 1917. A püspökfürdői preglaciális madárfauna [The pre-glacial bird fauna from Püspökfürdő, Hungary]. *Bar-langkutatás*, **5**, 66–74 [In Hungarian].

Carrera, L., Pavia, M., Peresani, M. & Romandini, M. 2018. Late Pleistocene fossil birds from Buso Doppio del Broion Cave (North-Eastern Italy): implications for palaeoecology, palaeoenvironment and palaeoclimate. *Bollettino della Società Paleontologica Italiana*, **57** (2), 145–174, https://doi.org/10.4435/BSPI.2018.10

Carrera, L., Pavia, M. & Varela, S. 2022. Birds adapted to cold conditions show greater changes in range size related to past climatic oscillations than temperate birds. *Scientific Reports*, **12**, 10813, https://doi.org/10.1038/s41598-022-14972-7

Chiffard, J., Delestrade, A., Yoccoz, N. G., Loison, A. & Besnard, A. 2019. Warm temperatures during cold season can negatively affect adult survival in an alpine bird. *Ecology and Evolution*, **9**, 12531–12543, https://doi.org/10.1002/ece3.5715

Clot, A., Brochet, G., Chaline, J., Desse, G., Evin, J., Granier, J., Mein, P., Mourer-Chauviré, C., Omnes, J. & Rage, J. C. 1984. Faune de la grotte préhistorique du bois du Cantet (Espèche, Hautes-Pyrénées, France). *Munibe Antropologia–Arkeologia*, **36**, 33–50.

Cramp, S. & Perrins, C. M. 1994. *The Birds of Western Palearctic*. Oxford University Press, Oxford, 1–1200.

Doan, K., Mackiewicz, P., Sandoval-Castellanos, E., Stefaniak, K., Ridush, B., Dalén, L., Węgleński, P. & Stankovic, A. 2018. The history of Crimean red deer population and *Cervus* phylogeography in Eurasia. *Zoological Journal of the Linnean Society*, **183** (1), 208–225, https://doi.org/10.1093/zoolinnean/zlx065

Doan, K., Niedziałkowska, M., Stefaniak, K. Sykut, M., Jędrzejewska, B., Ratajczak-Skrzatek, U., Piotrowska, N., Ridush, B., Zachos, Frank E., Popović, D., Baca, M., Mackiewicz, P., Kosintsev, P., Makowiecki, D., Charniauski, M., Boeskorov, G., Bondarev, A. A., Danila, G., Kusak, J., Rannamäe, E., Saarma, U., Arakelyan, M., Manaseryan, N., Krasnodębski, D., Titov, V., Hulva, P., Bălăşescu, A., Trantalidou, K., Dimitrijević, V., Shpansky, A., Kovalchuk, O., Klementiev, A. M., Foronova, I., Malikov, D. G., Juras, A., Nikolskiy, P., Grigoriev, S. E., Cheprasov, M. Y., Novgorodov, G. P., Sorokin, A. D., Wilczyński, J., Protopopov, A. V., Lipecki, G. & Stanković, A. 2022. Phylogenetics and phylogeography of red deer mtDNA lineages during the last 50 000 years in Eurasia. *Zoological Journal of the Linnean Society*, **194** (2), 431–456, https://doi.org/10.1093/zoolinnean/zlab025

Gąsiorowski, M., Hercman, H., Ridush, B. & Stefaniak, K. 2014. Environment and climate of the Crimean Mountains during the Late Pleistocene inferred from stable isotope analysis of red deer (*Cervus elaphus*) bones from the Emine-Bair-Khosar Cave. *Quaternary International*, **326–327**, 243–249, https://doi.org/10.1016/j.quaint.2013.12.020

Gavris, G. & Taykova, S. 2004. Aves from Karabi-Tamchin Cave. *ERAUL*, **104**, 295–298.

Jánossy, D. 1972. Middle Pliocene Microvertebrate fauna from the Osztramos Loc.1 (Northern Hungary). *Annales Historico Naturales Musei Nationalis Hungarici*, **64**, 27–48.

Jánossy, D. 1974. Die mittelpleistozäne Vogelfauna von Hundsheim (Niederösterreich). *Sitzungsberichte der Akademie der Wissenschaften mathematisch-naturwissenschaftliche Klasse*, **182**, 211–257.

Jánossy, D. 1979. Plio-Pleistocene bird remains from the Carpathian Basin. IV. Anseriformes, Gruiformes, Charadriiformes, Passeriformes. *Aquila*, **85**, 11–39.

Kessler, J. 2013. Neogene songbirds (Aves, Passeriformes) from Hungary. *Hantkeniana*, **8**, 37–149.

Kessler, J. 2020. Evolution of Corvids and their Presence in the Neogene and the Quaternary in the Carpathian Basin. *Ornis Hungarica*, **28** (1), 121–168.

Kessler, J. & Horváth, I. 2022. Presentation of so far undetermined bird remains from the Pliocene of Beremend 26 and Csarnóta 2 and 4 (Baranya county, South Hungary). *Ornis Hungarica*, **30** (1), 47–68.

Kostin, S. Yu. 2006. General aspects of Crimean avifauna. Communication 1. Experience of revision of avifaunal lists. *Branta*, **9**, 19–47 [In Russian, with English summary].

Kovalchuk, O., Rekovets, L., Tsvelykh, A., Yanenko, V., Manko, V. & Tajkova, S. 2021. Living in a time of change: Late Pleistocene / Holocene transitional vertebrate fauna of Grot Skeliastyi (Crimea, Ukraine). *Historical Biology*, **33** (10), 2074–2084, https://doi.org/10.1080/08912963.2020.1769094

Kretzoi, M. 1962. Madár-maradványok a betfiai alsópleisztocén faunából. *Aquila*, **67–68**, 167–174.

Kurochkin, E. N., Lopatin, A. V. & Zelenkov, N. V., eds. 2015. *Fossil vertebrates of Russia and adjacent countries. Part 3. Fossil reptiles and birds*. GEOS, Moscow [In Russian].

Laiolo, P. & Rolando, A. 1999. The diet of the chough (*Pyrrhocorax phyrrhocorax*) and the Alpine chough (*Pyrrhocorax graculus*) in the Alps: seasonality, resource partitioning and population density. *Revue d' Ecologie la Terre et la Vie*, **54** (2), 133–147.

Madge, S. 2019. Yellow-billed Chough (*Pyrrhocorax graculus*). *In*: del Hoyo, J., Elliot, A., Sargatal, J., Christie, D. A. & de Juana, E., eds. *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona, 1, https://doi.org/10.2173/bow.yebcho1.01

Majkić, A., Evans, S., Stepanchuk, V., Tsvelykh, A. & d'Errico, F. 2017. A decorated raven bone from the Zaskalnaya VI (Kolosovskaya) Neanderthal site, Crimea. *PLoS One*, **12** (3), e0173435, 1–33, https://doi.org/10.1371/journal.pone.0173435

Marco, A. S. 2018. Aves fósiles de la Península Ibérica, Canarias y Baleares: balance de los estudios realizados. *Boletín del Instituto Andaluz del Patrimonio Histórico*, **26**, 154–181.

McKay, C. R. 1996. *Conservation and ecology of the Red-Billed chough Pyrrhocorax pyrrhocorax.* Presented in candidature for the degree of Doctor of Philosophy in the Faculty of Science, University of Glasgow. Vol. I. University of Glasgow, 1–220+1–4.

Milne-Edwards, A. 1875. Observations sur les oiseaux dont les ossements ont été retrouvés dans les cavernes du Sud Ouest de la France. *Matériaux pour l'Histoire Primitive et Naturelle de l'Homme*, **6** (2), 473–503.

Mlíkovský, J. 1997. Late Pleistocene birds of Karlukovo, Bulgaria. *Historia naturalis bulgarica*, **7**, 59–60.

Mlíkovský, J. 2002. *Cenozoic birds of the World. Part 1: Europe*. Ninox press, Praha, 1–417.

Mlíkovský, J. 2009. Middle Pleistocene birds of Hundsheim, Austria. *Journal of the National Museum (Prague), Natural History*, **177** (7), 69–82.

Mourer-Chauviré, C. 1975. Les oiseaux du Pléistocène moyen et supérieur de France. *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon*, **64**, 1–624.

Murton, R. K. & Westwood, N. J. 1966. The foods of the Rock Dove and Feral Pigeon. *Bird Study*, **13** (2), 130–146.

Nikiforov, M. E. 2008. *Formation and structure of the avifauna of Belarus*. Belorusskaya nauka, Minsk, 1–297 [In Russian].

Niedziałkowska, M., Doan, K., Górny, M., Sykut, M., Stefaniak, K., Piotrowska, N., Jędrzejewska, B., Ridush, B., Pawełczyk, S., Mackiewicz, P., Schmölcke, U., Kosintsev, P., Makowiecki, D., Charniauski, M., Krasnodębski, D., Rannamäe, E., Saarma U., Arakelyan, M., Manaseryan, N., Titov, V., Hulva, P., Bălăşescu, A., Fyfe, R., Woodbridge, J., Trantalidou, K., Dimitrijević, V., Kovalchuk, O., Wilczyński, J., Obadă, T., Lipecki, G., Arabey, A. & Stanković, A. 2021. Winter temperature and forest cover have shaped red deer distribution in Europe and the Ural Mountains since the Late Pleistocene. *Journal of Biogeography*, **48**, 147–159. https://doi.org/10.1111/jbi.13989

Núñez-Lahuerta, C., Sauqué, V., Sanchis, A., Duarte, E. & de la Rasilla, M. 2021. Bird remains from the Middle Paleolithic levels (MIS3) of Llonin Cave (Peñamellera Alta, Asturias, Spain). *Comptes Rendus Palevol*, **20** (30), 627–640, https://doi.org/10.5852/cr-palevol2021v20a30

Potapova, O. R. & Baryshnikov, G. F. 1993. Birds from the Acheulean site in the Treugolnaya Cave in the North Caucasus. *Proceedings of the Zoological Institute of the Russian Academy of Sciences*, **249**, 48–65.

Rando, J. C. 2007. New fossil records of choughs genus *Pyrrhocorax* in the Canary Islands: hypotheses to explain its extinction and current narrow distribution. *Ardeola*, **54**, 185–195.

Ridush, B. 2013. *Paleogeographic reconstruction of the natural environment of the Late Cenozoic at the South of Eastern Europe after research of cave sediments*. Institute of Geography of the National Academy of Sciences of Ukraine, Kyiv. D. Sci. thesis, 1–45 [In Ukrainian].

Ridush, B., Stefaniak, K., Nadachowski, A., Ratajczak-Skrzatek, U., Socha, P., Popiuk, Y., Ridush, O. & Nykolyn, O. 2018. Pleistocene fauna of the Emine-Bair-Khosar Cave (Crimea, Ukraine): new data. *In*: Zupan Hajna, N., Mihevc, A., Năpăruș-Aljančič, M., eds. *Quaternary Stratigraphy in Karst and Cave Sediments. INQUA Section on European Quaternary Stratigraphy*. Karst Research Institute, Postojna, Slovenia, 57–59.

Ridush, B., Stefaniak, K., Socha, P., Proskurnyak, Y., Marciszak, A., Vremir, M. & Nadachowski, A. 2013. Emine-Bair-Khosar Cave in the Crimea, a huge bone accumulation of Late Pleistocene fauna. *Quaternary International*, **284**, 151–160, https://doi.org/10.1016/j.quaint.2012.03.050

Stankovic, A., Doan, K., Mackiewicz, P. et al. (7 more authors). 2011. First ancient DNA sequences of the Late Pleistocene red deer (*Cervus elaphus*) from the Crimea, Ukraine. *Quaternary International*, **245**, 262–267, https://doi.org/10.1016/j.quaint.2011.05.023

Suárez-Bilbao, A., Elorza, M., Castaños, J., Arrizabalaga, A., Iriarte-Chiapusso, M. J. & Murelaga, X. 2018. The Late Pleistocene avifauna from Artazu VII (Basque Country, northern Iberian Peninsula). *Historical Biology*, **32** (3), 307–320, https://doi.org/10.1080/08912963.2018.1491566

Tomek, T. & Bochenski, Z. M. 2000. *The Comparative Osteology of European Corvids (Aves: Corvidae), with a key to the identification of their skeletal elements*. Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, 1–102.

Tomek, T., Bochenski, Z. M., Socha, P. & Stefaniak, K. 2012. Continuous 300,000-year fossil record: changes in the ornithofauna of Biśnik Cave, Poland. *Palaeontologica Electronica*, **15** (1), 2A, https://doi.org/10.26879/277

Tsvelykh, A. N. 2013. Upper Pleistocene birds from the Zaskal'naya-IX Late Palaeolithic campsite and the avifauna of the Crimean foothills on the eve of the cold maximum of the Last Glacial. *Trudy Menzbirovskogo ornitologicheskogo obshchestva*, **2**, 110–119 [In Russian].

Tsvelykh, A. N. 2017. Revision of Late Pleistocene and Holocene Galliformes Fauna from the Crimean Mountains. *Biology Bulletin*, **44** (7), 761–768, https://doi.org/10.1134/S1062359017070160

Tsvelykh, A. N. 2018. Avifauna of archaeological layers II, III and IV. *In*: Stepanchuk, V. N., & Vasilyev, S. V., eds. *The Late Neanderthals of the Crimea. Zaskalnaya VI (Kolosovskaya), layers III and IIIa*. SLOVO, Kyiv, 73–76 [In Russian].

Tugarinov, A. 1937. The birds of Crimea during the Würm glaciation. *Trudy Sovetskoy Sektsii INQUA*, **1**, 97–114 [In Russian].

Tyrberg, T. 1991. Arctic, montane and steppe birds as glacial relicts in the West Palearctic. *Verhandlungen der Ornithologischen Gesellschaft in Bayern*, **25**, 29–49.

Tyrberg, T. 1998. *Pleistocene birds of the Palearctic: a catalogue*. Publications of the Nuttall Ornithological Club, No. 27. Nuttall Ornithological Club, Cambridge-Massachusetts, i–ix+1–720.

Villalta, J. F. 1964. Datos para un catálogo de las aves fósiles del cuaternario Español. *Speleon*, **15**, 79–102.

Voinstvensky, M. A. 1963. Fossil ornithofauna of the Crimea. *Trudy Kompleksnoy Karstologicheskoy Ekspeditsii AN USSR*, **1**, 106–122 [In Russian].

Voinstvensky, M. A. 1965. Some features of the modern avifauna of the Crimea and its history during the Anthropogene. *In*: Pidoplichko, I. G., ed. *Nazemni khrebetni Ukrainy* [*Terrestrial vertebrates of Ukraine*]. Naukova Dumka, Kyiv, 51–63 [In Ukrainian].

Voinstvensky, M. A. 1967. Fossil ornithofauna of Ukraine. *In*: Pidoplichko, I. G., ed. *Prirodnaya obstanovka i fauny proshlogo*, is. 3. Naukova Dumka, Kyiv, 3–76 [In Russian].

Vremir, M. & Ridush, B. 2005. The Emine-Bair-Khosar "Mega Trap" (Ukraine). *Mitteilungen der Kommission für Quartärforschung der Österreichischen Akademie der Wissenschaften*, **14**, 235–239.

Wojtal, P., Wilczyński, J., Bochenski, Z. M. & Svoboda, J. A. 2012. The scene of spectacular feasts: Animal remains from Pavlov I south-east, the Czech Republic. *Quaternary International*, **252**, 122–141, https://doi.org/10.1016/j.quaint.2011.06.033

Zelenkov, N. V. 2016 a. Revision of non-passeriform birds from Polgárdi (Hungary, Late Miocene): 1. Anseriformes. *Paleontological Journal*, **50** (5), 514–517.

Zelenkov, N. V. 2016 b. Revision of non-passeriform birds from Polgárdi (Hungary, Late Miocene): 2. Galliformes. *Paleontological Journal*, **50** (6), 623–634.

Zelenkov, N. V. 2017. Revision of non-passeriform birds from Polgárdi (Hungary, Upper Miocene): 3. Neoaves. *Paleontological Journal*, **51** (2), 203–213.

Received 19 December 2022
Accepted 22 March 2023