

Avifauna from the Neanderthal Site of Prepoštská jaskyňa Cave (Bojnice I) Near Prievidza – Biostratigraphical and Palaeoecological Implications

Mária Šedivá¹, Ján Obuch² & Martin Sabol¹

¹Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University in Bratislava, Ilkovičova Str. 6, SK – 84215 Bratislava, Slovak Republic; sediva20@uniba.sk, martin.sabol@uniba.sk

²Botanical Garden of the Comenius University in Bratislava, Blatnica Workplace, Blatnica 315, SK – 03815 Blatnica near Martin; obuch@rec.uniba.sk

AGEOS

Abstract: Prepoštská jaskyňa Cave (Bojnice I) near Prievidza is an archaeological site with confirmed Neanderthal settlements. The discovered fossil material, including also osteological remains of avifauna, comes from trenches II and III excavated by Juraj Bárta in 1965–1967. The evaluated fossil and subfossil bird remains from the Last Glacial Period to Holocene demonstrated a presence of 37 species from 11 orders. The studied material was divided into four assemblages, from which the most important is the northern *Lagopus*-assemblage typical for cold climatic conditions of the Last Glacial. Identified bird assemblages helped to reconstruct palaeoenvironmental and climatic conditions at the site and in its vicinity. The osteological material was also taphonomically evaluated indicating activity of various taphonomic agents.

Key words: Aves, palaeoenvironmental reconstruction, Quaternary stratigraphy, Prepoštská jaskyňa Cave, Slovakia

1. INTRODUCTION

Scientists have dealt with a bird fossil record minimally since 17th Century and so far, more than 600 Tertiary and 1,200 Pleistocene sites with an avifauna are known from the European territory. Apart from osteological remains, also feather imprints, endocasts, eggshell fragments, coprolites, and ichnofossils have been found (Mlíkovský, 1996, 2002). In addition to taxonomical importance, pointing out diversity of extinct bird assemblages, a fossil record of avifauna is also an important source for the palaeoenvironmental reconstructions.

So far, minimally 26 sites with the avifaunal fossil record are documented from karst and non-karst areas in the Slovakian territory. These localities are dated from the Early Oligocene up to the Late Pleistocene, and in total 73 different extant avian taxa together with four extinct ones have been found there (Šedivá, 2016).

A large amount of osteological bird material comes from excavations at archaeological sites. One of such localities is Prepoštská jaskyňa Cave in Bojnice (a castle townlet near Prievidza town) from which besides archaeological artefacts (Neruda & Kaminská, 2013) and non-avian zooarchaeological material (Čeklovský, 2014; Čeklovský et al., 2016), a large number of bird skeletal remains is also known (Čeklovský, 2015; Šedivá, 2018). This avian fossil record is analysed from the taxonomical point of view with the respect on biostratigraphical and palaeoecological outputs. However, it is important to note the sampling circumstances and the sedimentological settings are relatively complicated and often imprecise. Also, a basic taphonomic analysis is realized. However, the identification of human agents' activity, mainly of Neanderthals, is not a subject of this article.

2. LOCALITY

Prepoštská jaskyňa Cave is situated on the southern periphery of Bojnice (48° 46' 40" N, 18° 35' 00" E), SW of Bojnice castle (Fig. 1). The cave is located in a travertine cascade formed by activity of thermal springs (Fig. 2) and it is one of several so far discovered Neanderthal settlements in the Horná Nitra territory. It is currently a 11 metres wide, 4 to 8 metres high, and 7 metres deep (Neruda & Kaminská, 2013). Prepoštská jaskyňa Cave is not a typical karst cave and its origin is related to the sedimentation of the whole travertine body. The cave was formed by spring waters, flowing as waterfalls across the travertine wall. Later, the spring created a deeper underground communication and began to flow directly from the cave space (Ložek, 1962).

The first mention about the cave comes from provost K. A. Medvecký (1927). In 1926, he realized initial excavations and found shards of Slavic, Hallstatt, and Eneolithic pottery as well as hundreds of Palaeolithic artefacts and animal fossil bones, among them also bones and molar fragment of *Mammuthus primigenius* (Medvecký, 1927; Neruda & Kaminská, 2013). The first professional research was realized in 1927 in the entrance cave part with the participation of Š. Janšák, J. Skutil, J. Eisner, J. F. Babor and P. Deffontaine. According to J. Eisner (ex Medvecký, 1927), the cave was used by Palaeolithic hunters and served as a place for the stone tools manufacture. Before 1950, the site was often visited by amateur collectors. The first systematic archaeological field campaign at the site was realized by F. Prošek in 1950 (trench I; Fig. 3). His research confirmed the presence of the Middle Palaeolithic man – artefacts which were originally related to the Mousterian. From the palaeontological point of view, the cave lion mandible (*Panthera spelaea*) and the teeth



Fig. 1. Location of Prepoštská jaskyňa Cave (Bojnice I) in Slovakia near Prievidza town (white circle) (satellite map source: Google Earth; detailed map according to Bárta, 1972).

of woolly rhinoceros (*Coelodonta antiquitatis*) and mammoths belong among the most interesting discoveries (Prošek, 1952; Neruda & Kaminská, 2013).

From 1965 to 1967, J. Bárta continued in the field research of the site (Bárta, 1972). He opened a new trench inside the cave (trench II) situated west of Prošek's trench and also focused



Fig. 2. Neanderthal site of Prepoštská jaskyňa Cave (Bojnice I): A – historical view of the site from the first half of the 20th Century (<https://muzeumpravku.sk/wp-content/uploads/2010/12/jask.jpg>, 20.01.2020), B, D – nowadays views, C – detail view of the site with a reconstruction of Neanderthal settlement.

his research on a small space in the eastern part of the cave abri called “Kostnica” (= Charnel-House; trench III, divided into partial trenches IIIa to IIId). The precise location of individual trenches is on Fig. 3.

The “Kostnica” was not suitable for the settlement and it served rather as a waste pit (Neruda & Kaminská, 2013). Apart from archaeological artefacts, a rich faunal assemblage was found here (Čeklovský, 2015), with many bird skeletal elements. These were preliminary determined by Dr. D. Jánossy in 1965 for purpose of vertebrate analysis carried out by Prof. O. Fejfar. He determined six bird taxa coming from four layers – Anatidae and Charadriidae were found in the layer 2, species *Surnia ulula* was identified in the layer 3, *Lagopus* aff. *lagopus* was found together with Corvidae gen. et spec. indet. in the layer 4, and layer 6 yielded remains of *Lyrurus tetrrix* (ex Neruda & Kaminská, 2013: p. 200). A more detailed taxonomical summary of bird remains from the excavations of J. Bárta and J. Eisner (or Š. Janšák) was later published by T. Čeklovský in his PhD thesis (2015), where he determined 23 bird taxa, but without more detailed palaeoecological analysis except for two species (*Lagopus lagopus* and *Bubo scandiacus*).

3. MATERIAL AND METHODS

The osteological material under study is housed in the Horná Nitra Museum in Prievidza. It was collected from layers of Pleistocene and Holocene ages of trenches II and III during the research of J. Bárta in years 1965–1967 (Fig. 3). The material is labeled as A-IX 715/7 to A-IX 900/72.

The sampling in trench II was carried out by 5 cm. Concerning the trench III, the predominantly horizontal position of animal bones in partial trench IIIa was interpreted as primary, while the bone orientation in partial trench IIIb points rather to the “waste character” of the “Kostnica” area, as it has already been mentioned by Bárta in his manuscript on p. 52 (ex Neruda & Kaminská, 2013). The material was probably affected by redeposition which caused mixing of bones of various ages (Čeklovský, 2015).

The bird remains were found mainly in trench III, occasionally also in trench II (Tab. 1). The bird bones and their fragments are mostly hollow, thin-walled, and show predominantly a low degree of fossilization. They vary in colour, from light brown or light orange to orange, grey and dark brown. A significant portion is damaged, with the different types of fractures (irregular perpendicular and spiral ones predominate, see below). Since this material deposited in the museum collections was in a bad state, it was fixed by a solution of water and Duvilax dispersion adhesive (realized by T. Čeklovský).

The traditional morphometric analysis (Marcus, 1990) was used to evaluate the osteological material. Biometrics was realized by standard method using the Powerfix digital caliper (Model No. Z22855F) with a maximum range of 15 cm and 0.01 mm accuracy according to the methodology of Ellenberger and Baum (1943). The morphological terminology was adopted from the work of Popesko (1992). The definition of individual anatomical elements and full detailed description of each bone

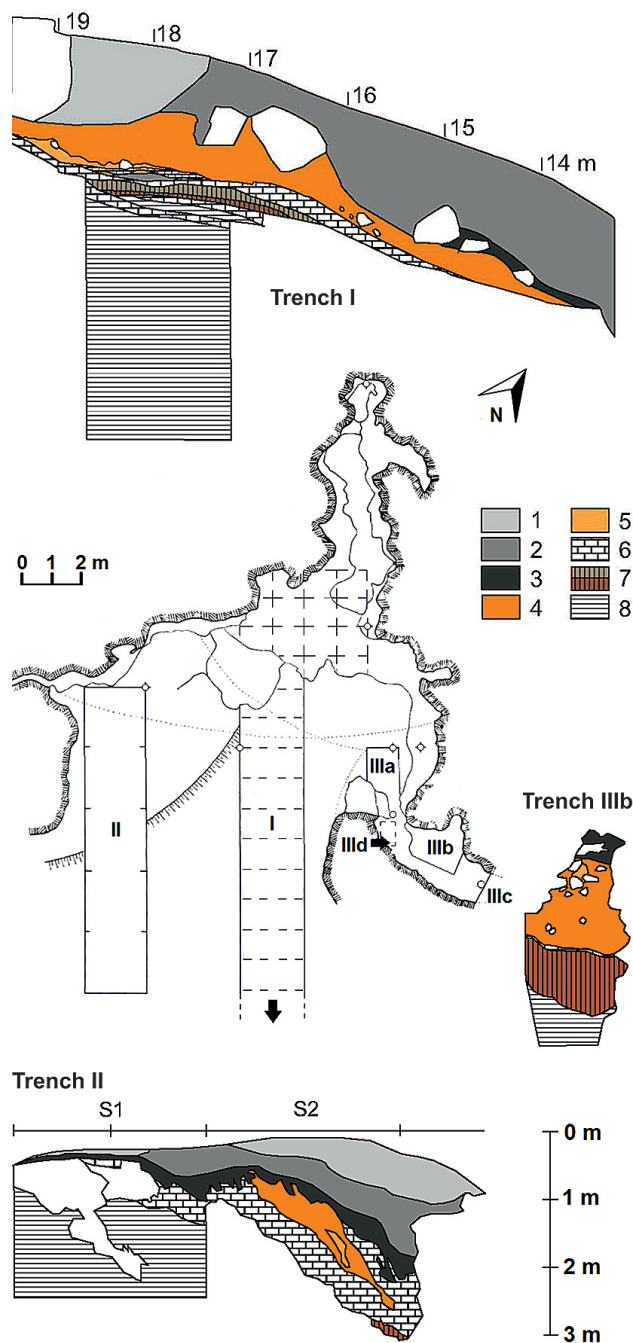


Fig. 3. Ground plan of Prepošťská jaskyňa Cave with profiles of three excavated trenches – trench I (Prošek’s trench from 1950), trench II (Bárta’s trench from 1960s) and trench III (“Kostnica”) divided to partial trenches a–d (Bárta’s trench from 1960s). The crosses in ground plan indicate the area of Janšák’s excavation in 1927. Modified according to Prošek (1952), Bárta (original documentation), Neruda & Kaminská (2013), and Čeklovský (2015). The smaller scale is for the ground plan, the larger one is for trench profiles.

Abb.: 1 – grey-brown relocated sediment of the previous excavations; 2 – grey-brown landfill; 3 – dark grey humous soil; 4 and 5 (cultural layers) – yellow-brown loess loam; 6 – white-grey travertine plate; 7 (cultural layer) – discontinuous travertine, grey to grey-brown in surface portion, light-brown to brown in its base; 8 – white-grey to yellow non-cohesive travertine-foam sinter.

Tab. 1. List of bird taxa from trenches II and III of Bárta. Data in grey lines and columns probably indicate the Holocene record. The “Total” line for trench III consists of three sub-lines – the upper one indicates the total number of bird finds in separate depths, the middle sub-line indicates the total number of bird finds in single parts of trench III, and the lower sub-line indicates the total number of bird remains in this trench.

Taxon (NISP/MNI)	Trenches																								
	II.		III.																	?					
	IIIa		IIIb											IIIc											
	0-15 cm	15-30 cm	113-122 cm	120-135 cm		130-140 cm	135-150 cm	150-170 cm (layer 2)	160-170 cm	170-175 cm	entrance 2 m	200-210 cm	210-230 cm	220-230 cm	230-240 cm	240-310 cm	?	30-40 cm	40-50 cm		50-60 cm	80-110 cm	100-110 cm	120-130 cm	
<i>Anas platyrhynchos</i> (6/2)										4			1											1	
<i>Bucephala clangula</i> (3/3)																	1							2	
<i>Coturnix coturnix</i> (2/1)					1															1					
<i>Gallus sp.</i> (2/1)																				1				1	
<i>Lagopus lagopus</i> (34/11)	2		1	1				3		3	1						5		1		1		1	15	
<i>Lagopus muta</i> (18/7)	3							2											1				1	11	
<i>Lyrurus tetrix</i> (30/6)		1				1	3			1							4						1	19	
<i>Phasianus colchicus</i> (1/1)																								1	
<i>Tetrao urogallus</i> (3/2)										1														2	
<i>Columba palumbus</i> (1/1)								1																	
<i>Crex crex</i> (11/2)		1		1	1	1			1	1								1					1	3	
<i>Fulica atra</i> (1/1)																1									
<i>Gallinula chloropus</i> (1/1)																								1	
<i>Vanellus vanellus</i> (2/1)																								2	
<i>Gallinago gallinago</i> (2/1)								1																1	
<i>Numenius arquata</i> (1/1)											1														
<i>Numenius phaeopus</i> (1/1)																								1	
<i>Philomachus pugnax</i> (1/1)								1																	
<i>Tachymarptis melba</i> (4/2)				1				1	1						1										
<i>Accipitriformes indet.</i> (2/1)										1		1													
<i>Strix uralensis</i> (1/1)	1																								
<i>Asio otus</i> (1/1)																	1								
<i>Asio flammeus</i> (2/1)												1					1								
<i>Bubo bubo</i> (1/1)																								1	
<i>Athene noctua</i> (1/1)																								1	
<i>Falco columbarius</i> (1/1)																								1	
<i>Falco tinnunculus</i> (2/1)																								2	
<i>Corvus corax</i> (1/1)		1																							
<i>Coloeus monedula</i> (4/2)	1		1				1	1																	
<i>Pyrrhocorax sp.</i> (1/1)															1										
<i>Garrulus glandarius</i> (2/1)				1																				1	
<i>Nucifraga caryocatactes</i> (1/1)							1																		
<i>Turdus merula</i> (1/1)				1																					
<i>Turdus iliacus</i> (1/1)																								1	
<i>Turdus pilaris</i> (3/1)				1			1																	1	
<i>Turdus viscivorus</i> (1/1)							1																		
<i>Pinicola enucleator</i> (1/1)																								1	
<i>Coracias garrulus</i> (1/1)																						1			
Total	6	2	2	2	1	7	2	7	10	1	2	10	2	2	1	1	2	12	1	2	2	1	1	4	69
		4								62										11					

can be found in the diploma thesis of Šedivá (2018). Taxonomic determination of skeletal remains was based on morphological and metric comparisons with collections of one of the co-authors (JO). The ornithological terminology was adopted from the work of Kovalik et al. (2010) and various taphonomic phenomena reported on bones (see below) have been analysed primarily according to Lyman (1996).

4. RESULTS

4.1. Avian assemblages

The zooarchaeological material (Figs. 4–7) contains osteological remains of 37 bird species from 30 genera and 11 orders. These are attributed into families Anatidae (*Anas platyrhynchos*, *Bucephala clangula*), Phasianidae (*Coturnix coturnix*, *Gallus* sp., *Lagopus lagopus*, *L. muta*, *Lyrurus tetrrix*, *Phasianus colchicus*, *Tetrao urogallus*), Columbidae (*Columba palumbus*), Ralidae (*Crex crex*, *Fulica atra*, *Gallinula chloropus*), Charadriidae (*Vanellus vanellus*), Scolopacidae (*Gallinago gallinago*, *Numenius arquata*, *N. phaeopus*, *Philomachus pugnax*), Apodidae (*Tachymarptis melba*), Strigidae (*Strix uralensis*, *Asio otus*, *A. flammeus*, *Bubo bubo*, *Athene noctua*), Falconidae (*Falco columbarius*, *F. tinnunculus*), Corvidae (*Corvus corax*, *Coloeus monedula*, *Pyrrhocorax* sp., *Garrulus glandarius*, *Nucifraga caryocatactes*), Turdidae (*Turdus merula*, *T. iliacus*, *T. pilaris*, *T. viscivorus*), Fringilidae (*Pinicola enucleator*), and Coraciidae (*Coracias garrulus*) (see Supplement 1).

Because all determined taxa live in Europe till today, they can be grouped in several assemblages based on their geographical distribution and the habitats they now inhabit by using the actualistic principles.

Based on the geographical distribution in Europe and adjacent areas, four assemblages were distinguished: (1) **northern assemblage**, which includes *Lagopus lagopus*, *L. muta*, *Lyrurus tetrrix*, *Tetrao urogallus*, *Numenius phaeopus*, *Strix uralensis*, *Pinicola enucleator*, and *Nucifraga caryocatactes*; norse but migratory species are also *Turdus pilaris*, *T. iliacus*, *Bucephala clangula*, and *Falco columbarius*; (2) **intermediate, or migratory assemblage** resp., including *Crex crex*, *Gallinula chloropus*, *Vanellus vanellus*, *Gallinago gallinago*, *Philomachus pugnax*, *Fulica atra*, *Coturnix coturnix*, and *Turdus viscivorus*; (3) **assemblage of cosmopolitan species** such as *Anas platyrhynchos*, *Numenius arquata*, *Falco tinnunculus*, *Bubo bubo*, *Asio flammeus*, *A. otus*, *Coloeus monedula*, *Corvus corax*, *Garrulus glandarius*, *Columba palumbus*, or *Turdus merula*; and (4) **southern assemblage**, which may include *Tachymarptis melba*, *Coracias garrulus*, *Pyrrhocorax* sp., and *Athene noctua*.

Based on the environment in which the individual species live today, these can be divided as follows: (a) **aquatic species** (*Anas platyrhynchos*, *Bucephala clangula*, *Fulica atra*, and *Gallinula chloropus*); (b) **forest species** (*Tetrao urogallus*, *Lyrurus tetrrix*, *Columba palumbus*, *Strix uralensis*, *Asio otus*, *Corvus monedula*, *Garrulus glandarius*, *Nucifraga caryocatactes*, *Turdus merula*, *T. iliacus*, *T. pilaris*, *T. viscivorus*, and *Pinicola enucleator*); (c) **species living in meadows and grassland** (*Coturnix coturnix*); (d) **species inhabiting meadows and**

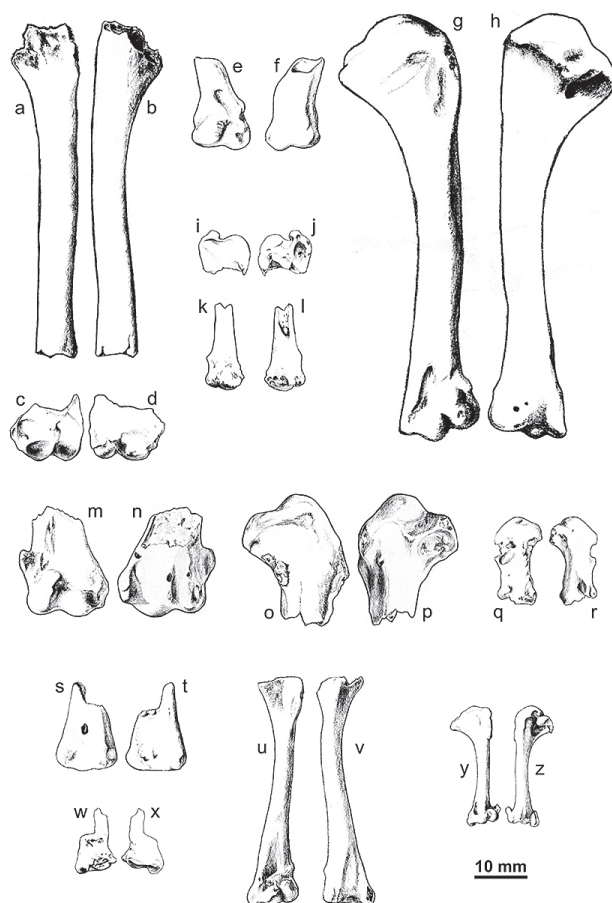


Fig. 4. Fragmented and complete avian humeri from Quaternary deposits of Prepoštská jaskyňa Cave. a–d) *Anas platyrhynchos* – a–b: diaphysis of the left humerus (A-IX 728/19, a – lateral view, b – medial view), c–d: distal epiphysis of the left humerus (A-IX 779/5, c – lateral view, d – medial view); e–f) *Lagopus muta*: distal portion of the right humerus (A-IX 843/26, e – lateral view, f – medial view); g–h) *Lyrurus tetrrix*: left humerus (A-IX 778/12, g – lateral view, h – medial view); i–l) *Gallinago gallinago* – i–j: proximal epiphysis of the left humerus (A-IX 900/43, i – lateral view, j – medial view), k–l: distal portion of the right humerus (A-IX 843/27, k – lateral view, l – medial view); m–n) *Numenius arquata*: distal portion of the right humerus (A-IX 773/2, m – lateral view, n – medial view); o–p) *N. phaeopus*: proximal portion of the left humerus (A-IX 849/31, o – lateral view, p – medial view); q–r) *Tachymarptis melba*: right humerus (A-IX 776/1, q – lateral view, r – medial view); s–t) *Asio otus*: distal portion of the right humerus (A-IX 820/30, s – lateral view, t – medial view); u–v) *Falco tinnunculus*: left humerus (A-IX 893/5, u – lateral view, v – medial view); w–x) *Nucifraga caryocatactes*: distal portion of the left humerus (A-IX 898/27, w – lateral view, x – medial view); y–z) *Pinicola enucleator*: left humerus (A-IX 887/51, y – lateral view, z – medial view).

pastures close to smaller forests (*Athene noctua* and *Falco tinnunculus*); (e) **species inhabiting waterlogged meadows and/or marshes** (*Crex crex*, *Vanellus vanellus*, *Gallinago gallinago*, *Numenius arquata*, *N. phaeopus*, *Philomachus pugnax*, *Asio flammeus*, and *Coracias garrulus*); (f) **species inhabiting mountains and mountain ranges** (*Tachymarptis melba*, *Bubo bubo*, *Corvus corax*, and *Pyrrhocorax* sp.); and (g) **species inhabiting tundra, forest-tundra and taiga** (*Lagopus lagopus*, *L. muta*, *Falco columbarius*) (Hume, 2004).

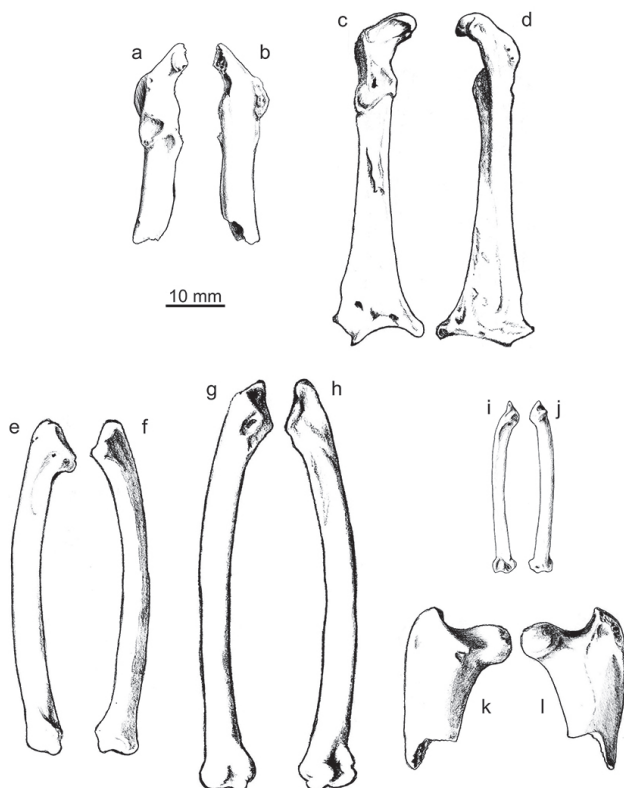
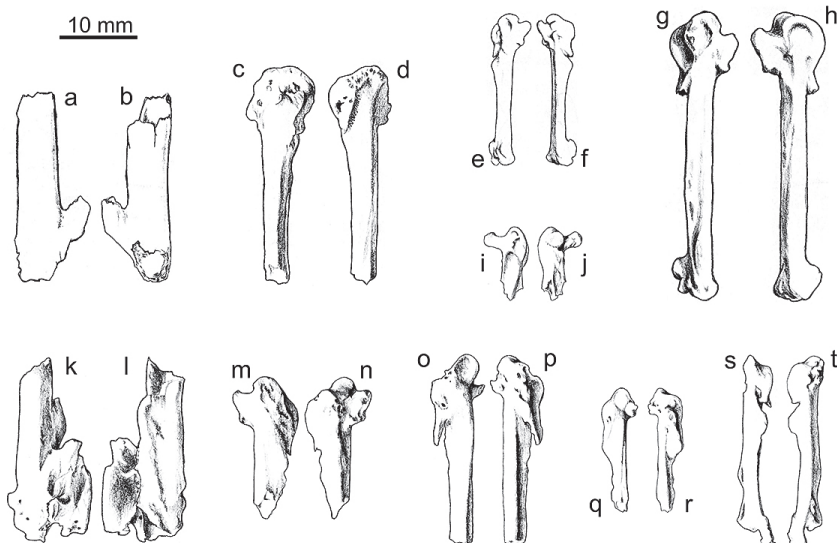


Fig. 5. Osteological remains of birds from Quaternary deposits of Prepoštská jaskyňa Cave. a–d) *Anas platyrhynchos*: proximal portion of the left coracoid (A-IX 724/9, a – caudal view, b – cranial view); c–d) *Gallus* sp.: left coracoid (A-IX 718/7, a – caudal view, b – cranial view); e–f) *Lagopus lagopus*: left ulna (A-IX 897/10, a – medial view, b – lateral view); e–f) *Lyrurus tetrix*: left ulna (A-IX 884/10, a – medial view, b – lateral view); i–j) *Turdus iliacus*: left ulna (A-IX 885/22, a – medial view, b – lateral view); k–l) *Tetrao urogallus*: proximal portion of the left femur (A-IX 837/21, a – caudal view, b – cranial view).

Fig. 6. Fragmented and complete avian metacarpal bones (II+III) from Quaternary deposits of Prepoštská jaskyňa Cave. a–d) *Anas platyrhynchos*: fragmented distal portion of the left metacarpal bone (A-IX 724/15, a – lateral view, b – medial view); c–d) *Columba palumbus*: proximal portion of the left metacarpal bone (A-IX 898/28, c – lateral view, d – medial view); e–f) *Coturnix coturnix*: right metacarpal bone (A-IX 897/16, e – lateral view, f – medial view); g–h) *Gallinula chloropus*: right metacarpal bone (A-IX 885/24, g – lateral view, h – medial view); i–j) *Philomachus pugnax*: proximal portion of the left metacarpal bone (A-IX 900/55, i – lateral view, j – medial view); k–l) *Corvus corax*: fragmented distal portion of the left(?) metacarpal bone (A-IX 772/2, k – lateral view, l – medial view); m–n) *Coloeus monedula*: proximal portion of the left metacarpal bone (A-IX 900/54, m – lateral view, n – medial view); o–p) *Garrulus glandarius*: proximal portion of the right metacarpal bone (A-IX 897/15, o – lateral view, p – medial view); q–r) *Turdus merula*: proximal portion of the right metacarpal bone (A-IX 897/30, q – lateral view, r – medial view); s–t) *Turdus viscivorus*: left metacarpal bone (A-IX 898/29, s – lateral view, t – medial view).



The northern hawk-owl (*Surnia ulula*), also known from the site based on previous determination by Jánossy in 1965 (ex Neruda & Kaminská, 2013), is a typical boreal forest species, living predominantly in open coniferous forest or coniferous forest mixed with deciduous species. It generally avoids dense spruce-fir forests and can also occur in muskegs, clearings, swamp valleys, and meadows.

Overall, Prepoštská jaskyňa Cave is dominated by the forest assemblage along with the northern assemblage of tundra and taiga (Figs. 8 and 9).

4.2. Biostratigraphy and palaeoecology

As mentioned above, only osteological remains of birds from trenches II and III have been analyzed here (Tab. 1).

The deposits of the trench II contained in unknown depth the remains of species such as *Lagopus lagopus*, *L. muta*, and *Strix uralensis*, indicating cold climate and presence of open environment with scattered forest growths. Most likely, these come from the cultural layer D, where a greater number of avifauna fossil remains have been reported (Neruda & Kaminská, 2013: p. 48). The associated assemblages of small mammals (Fejfar ex Neruda & Kaminská, 2013: p. 200) and terrestrial gastropods (Prošek & Ložek, 1951) indicate a cold steppe environment. The only dated bone from the burnt-bone horizon (OxA-22458) of this culture layer yielded an age older than 45,800 BP (Neruda & Kaminská, 2013: Tab. 1). Based on that, the determined bird assemblage can be dated to the MIS 3 period, probably to one of its non-forested interstadials, older than Hengelo (possibly Moershoofd or Glinde) (Tab. 2).

The material from partial trench IIIa came from two specified depths. Osteological remains assigned to *Crex crex* and *Coloeus monedula* were found in the uppermost 15 cm, while the record of *Lyrurus tetrix* and *Corvus corax* came from the depth of 15 to

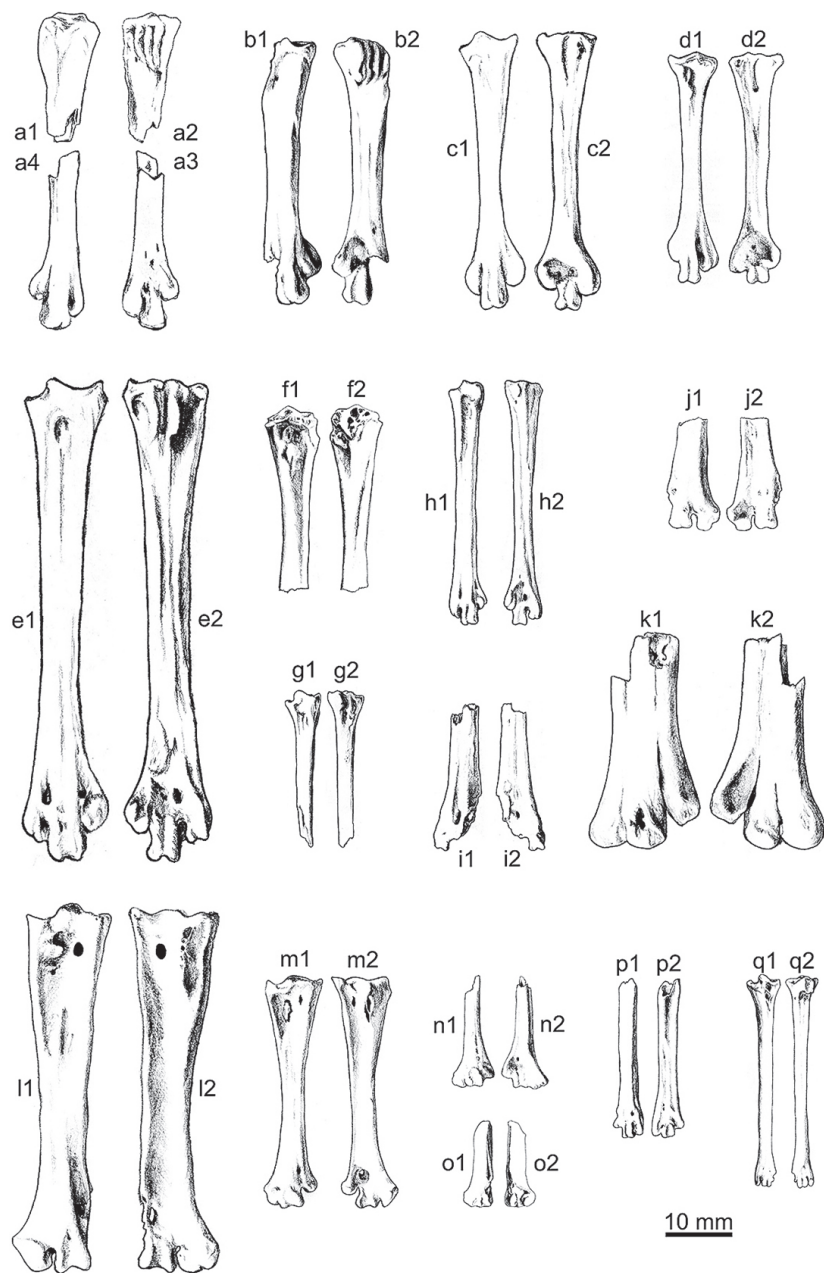


Fig. 7. Fragmented and complete avian tarsometatarsal bones from Quaternary deposits of Prepošťská jaskyňa Cave. a1–4) *Anas platyrhynchos*: a1–2 – proximal portion of the left tarsometatarsal bone (A-IX 774/25, a1 – dorsal view, a2 – ventral view), a3–4 – distal portion of the left tarsometatarsal bone (A-IX 842/52, a3 – dorsal view, a4 – ventral view); b1–2) *Bucephala clangula*: damaged right tarsometatarsal bone (A-IX 814/4, b1 – dorsal view, b2 – ventral view); c1–2) *Lagopus lagopus*: right tarsometatarsal bone (A-IX 887/54, c1 – dorsal view, c2 – ventral view); d1–2) *Lagopus muta*: left tarsometatarsal bone (A-IX 896/18, d1 – dorsal view, d2 – ventral view); e1–2) *Phasianus colchicus*: right tarsometatarsal bone (A-IX 887/53, e1 – dorsal view, e2 – ventral view); f1–2) *Tetrao urogallus*: proximal portion of the left tarsometatarsal bone (A-IX 874/1, f1 – dorsal view, f2 – ventral view); g1–2) *Vanellus vanellus*: proximal portion of the right tarsometatarsal bone (A-IX 889/1, g1 – dorsal view, g2 – ventral view); h1–2) *Crex crex*: right tarsometatarsal bone (A-IX 863/21, h1 – dorsal view, h2 – ventral view); i1–2) *Fulica atra*: fragmented distal portion of the right tarsometatarsal bone (A-IX 779/1, i1 – dorsal view, i2 – ventral view); j1–2) *Asio flammeus*: fragmented distal portion of the right tarsometatarsal bone (A-IX 820/21, j1 – dorsal view, j2 – ventral view); k1–2) *Bubo bubo*: distal portion of the left tarsometatarsal bone (A-IX 843/25, k1 – dorsal view, k2 – ventral view); l1–2) *Strix uralensis*: left tarsometatarsal bone (A-IX 887/56, l1 – dorsal view, l2 – ventral view); m1–2) *Athene noctua*: left tarsometatarsal bone (A-IX 720/3, m1 – dorsal view, m2 – ventral view); n1–2) *Falco columbarius*: distal portion of the left tarsometatarsal bone (A-IX 883/14, n1 – dorsal view, n2 – ventral view); o1–2) *Coracias garrulus*: fragmented distal portion of the left tarsometatarsal bone (A-IX 766/1, o1 – dorsal view, o2 – ventral view); p1–2) *Pyrhocorax* sp.: damaged right tarsometatarsal bone (A-IX 763/1, p1 – dorsal view, p2 – ventral view); q1–2) *Turdus pilaris*: right tarsometatarsal bone (A-IX 882/41, q1 – dorsal view, q2 – ventral view).

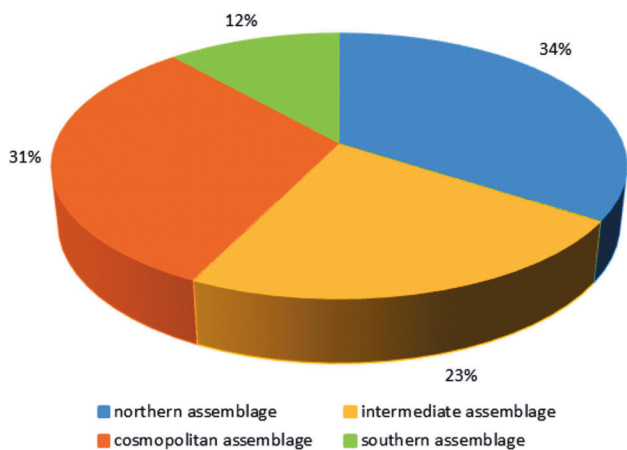


Fig. 8. The percentage of avian assemblages from Prepošťská jaskyňa Cave based on the geographical distribution in Europe and adjacent areas.

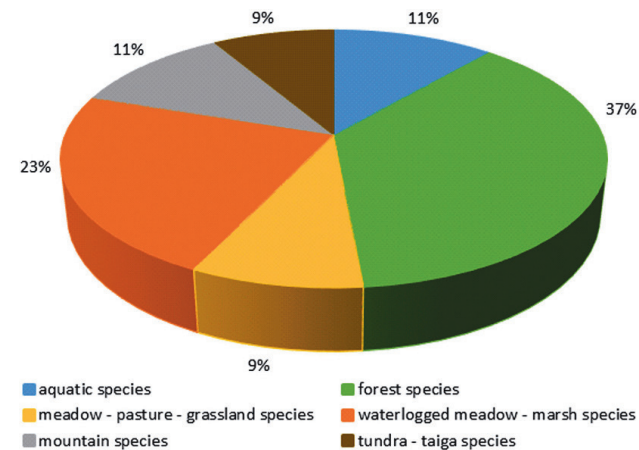


Fig. 9. The distribution of avian species from Prepošťská jaskyňa Cave on their present-day habitats.

30 cm. According to the accessible documentation, the surrounding sediment was a brown soil, probably of the Holocene age (at least material from the depth 0–15 cm), indicating a temperate climate with forest environment with the presence of wetter areas (Tab. 2).

Material from the partial trench IIIb, come from a depth of 113 to 310 cm, what corresponds to the vertical position of layers B to E distinguished in this part by Neruda & Kaminská (2013: Fig. 25 B–C). Unlike the partial trench IIIa, the material from IIIb bears signs of a redeposition. The culture layer B with an average thickness of 100 cm is approximately situated in a depth from 50 to 150 cm, or up to 170 cm respectively. This layer consists of yellow-brown loess clay with collapsed travertine blocks, sporadic malacofauna, pieces of pine charcoals, Palaeolithic industry and fossil bones (Neruda & Kaminská, 2013). From the depth of 113 to 122 cm, the osteological remains of *Lagopus lagopus* and *Coloeus monedula* are known; at a depth of 122 to 150 cm, the same species are accompanied by *Lyrurus tetrrix*, *Coturnix coturnix*, *Columba palumbus*, *Crex crex*, *Tachymarpis melba*, *Garrulus glandarius*, *Nucifraga caryocatactes*, *Turdus merula*, and *T. viscivorus*. Material from a depth of 150 to 170 cm, which is marked in the original documentation of J. Bárta as “layer 2”, can also be associated with this culture layer. It contains *L. lagopus*, *L. muta*, *Gallinago gallinago*, *Philomachus pugnax*, *T. melba*, *C. monedula*, and *T. pilaris*. The bird assemblage from the culture layer B indicates an open steppe landscape in a vicinity of the site with possible passage to tundra (based on finds of cold-loving species from the *Lagopus* assemblage) with both dry and waterlogged grassland or marsh meadows (sought after by species such as *Gallinago gallinago*, *Philomachus pugnax*, *Crex crex* and *Coturnix coturnix*). Islets of forest vegetation dwelled by *Nucifraga caryocatactes*, *Coloeus monedula*, *Columba palumbus*, *Turdus merula*, *T. pilaris*, and *Garrulus glandarius* could also be present (Tab. 2). However, the question is raised by the occurrence of *T. melba*, since this bird is rather a southern and alpine species, inhabiting primarily the warm temperate to subtropical zone. Either the surroundings of the locality with the thermal travertine spring at that time provided suitable conditions for its life, or its presence was accidental, and it could only appear here when flying to another suitable habitat within its migration route. The presence of gastropod *Helix pomatia*, which was noted by J. Bárta in his sketch profile at the top of this cultural layer (ex Neruda & Kaminská, 2013: Fig. 25C) is also interesting. This molluscan species indicates a warm temperate climatic condition.

Sample from depth 200 to 240 cm already likely comes from the culture layer D. This interval consists of a white to gray-yellow foam sinter with a lower occurrence of the Palaeolithic stone industry. The bird assemblage consists of *Anas platyrhynchos*, *Lagopus lagopus*, *Fulica atra*, *Numenius arquata*, *Asio flammeus*, and an unspecified representative of the Accipitriformes family. This assemblage indicates both the tundra environment and waterlogged grasslands or marshes with open water bodies (Tab. 2).

Bird remains from the lowest interval (240–310 cm) of the partial trench IIIb belong to layer E, and are accompanied with sporadic Palaeolithic artifacts (Neruda & Kaminská, 2013). The

sediment is a lighter whitish, grayish-yellow foam sinter which yielded remains of *Tachymarpis melba* and *Pyrrhocorax* sp.. These taxa currently inhabit mostly mountain ranges in southern Europe, but can fly to our territory or migrate through it in that period. This interval can be correlated with the layer H of trench II, which Neruda and Kaminská (2013) correlate with layer 7 of trench I. This layer was originally dated by Prošek (1952) to the beginning of the Last Glacial (W1). Based on the terrestrial mollusc species found, the climate was drier, indicating an existence of steppe habitats (Prošek & Ložek 1951).

The “special assemblage” comes from the sample from the same partial trench IIIb, labeled by J. Bárta as “entrance 2 m”. Probably, it represents the layers B and D. The osteological remains were assigned to the taxa *Anas platyrhynchos*, *Tetrao urogallus*, *Lyrurus tetrrix*, *Lagopus lagopus*, and Accipitriformes gen. et spec. indet., indicating a boreal environment of the Last Glacial.

Some material from the partial trench IIIb lacks precise stratigraphical position; this concerns *Bucephala clangula*, *Lyrurus tetrrix*, *Lagopus lagopus*, *Asio otus*, and *A. flammeus*. Their existence can be also associated with colder climatic and ecological conditions.

Bird remains from partial trench IIIc come from a depth 30 to 130 cm. The depth interval from 30 to 40 cm yielded only a single specimen, belonging to *Crex crex*. At the depth of 40 to 50 cm, bones of *Lagopus lagopus* and *L. muta* were uncovered and fossils of these species were also recorded at the depth of 120 to 130 cm together with remains of *Crex crex* and *Lyrurus tetrrix*. Osteological remains of taxa *Coturnix coturnix* and *Gallus* sp. were recorded at the depth of 50 to 60 cm and the willow ptarmigan (*L. lagopus*) was found even at the depth of 80 to 110 cm. These species (except for *Gallus* sp.) indicate a grassland to boreal forest environment and somewhat cooler climate than today and can be considered to have come from the Last Glacial Period (Tab. 2). The record of the species *Coracias garrulus* from the depth of 100 to 110 cm is also interesting. This thermophilous species lives in Slovak territory today only during the summer months and its presence on the site during the Last Glacial can only be associated with a warm oscillation (an interstadial) during MIS 3. The record from the partial trench IIIc, similarly to IIIb, indicates a “mixing” of material from different periods. Unfortunately, many bird remains from IIIc lacks detailed sampling location (Tab. 1). These remains are attributed to the following species: *Anas platyrhynchos*, *Bucephala clangula*, *Tetrao urogallus*, *Lyrurus tetrrix*, *Lagopus muta*, *L. lagopus*, *Crex crex*, *Gallinula chloropus*, *Vanellus vanellus*, *Gallinago gallinago*, *Numenius phaeopus*, *Bubo bubo*, *Athene noctua*, *Falco tinnunculus*, *F. columbarius*, *Garrulus glandarius*, *Turdus pilaris*, *T. iliacus*, *Pipicola enucleator*, *Phasianus colchicus* and *Gallus* sp.. The last two taxa are probably already of the Recent origin.

Except for part IIIa, the trench III can be described as a “waste pit”. Moreover, the redeposition of the material by water most likely caused a mixture of Pleistocene and Holocene remains. This is also evidenced by the obtained ¹⁴C data published in Neruda and Kaminská (2013) and Čeklovský et al. (2016), ranging from 3,071 ± 30 years BP (OxA-22459), through 24,677 ± 127 years BP (ETH-51814) and 33,697 ± 310 to

Tab. 2. Correlation stratigraphic scheme of avian fossil record from trenches II and III from Prepoštská jaskyňa Cave with the focus on palaeoenvironmental conditions (data source: Prošek, 1952; Neruda & Kaminská, 2013). “Lagopus-assemblage” includes species found in the partial trench IIIb at the depth of 113 to 170 cm (see Tab. 1).

Trenches					Environment	Age Series
II	III			Layers		
Layers	IIIa	IIIb	IIIc	Layers		
A (5 - 25 cm)	grey-brown relocated sediment	dark grey humous soil	<i>Crex crex</i> , <i>Coloeus monedula</i> ; <i>Lyrurus tetrrix</i> , <i>Corvus corax</i>	A (50 cm)	forest	HOLOCENE
B (15 cm)						
C (8 - 10 cm)	<i>L. lagopus</i> , <i>L. muta</i>	grassland to boreal forest				
D (18 cm)	yellow-brown loess loam (cultural layers)		<i>Lagopus lagopus</i> , <i>L. muta</i> , <i>Lyrurus tetrrix</i> , <i>Crex crex</i> , <i>Coracias garrulus</i>	B (1 - 1,2 m)	cold steppe steppe to tundra (± open forest)	boreal environment
E (5 cm)		"Lagopus - assemblage"				
F (15 - 20 cm)	grey travertine	<i>Anas platyrhynchos</i> , <i>Lagopus lagopus</i> , <i>Lyrurus tetrrix</i> , <i>Tetrao uragallus</i> , <i>Fulica atra</i> , <i>Numenius arquata</i> , <i>Asio flammeus</i> , <i>Accipitriformes</i> indet.		C (8 cm)	tundra - wet grassland to marshes	PLEISTOCENE
G (5 cm)				D (80 cm)		
H (70 cm)	white-grey to yellow non-cohesive travertine-foam sinter	<i>Tachymarpitis melba</i> , <i>Pyrrhocorax</i> sp.		E (> 50 cm)	steppe wet (swamp?)	

- grey-brown relocated sediment
- dark grey humous soil
- yellow-brown loess loam (cultural layers)
- grey travertine
- white-grey to yellow non-cohesive travertine-foam sinter

37,749 ± 516 years BP (ETH-51815 – ETH-51818, ETH-57301, ETH-57302) up to 44,800 to > 49,000 years BP (OxA-22456, OxA-22457).

4.3. Taphonomy

Only basic taphonomic analysis has been carried out, focusing mainly on the evaluation of fracture types and on the activity of various biotic and abiotic agents, influencing the bone colouring, surface structure, or shape changes.

The bones are often mineralized with manganese or iron oxides, which may form discontinuous coatings or characteristic dendrite pattern (less common). The coatings are the result of penetration of manganese compounds contained in cave water and cave sediments. These may also indicate relatively warm climatic conditions in which dark minerals such as amphiboles, pyroxenes and biotite are weathered.

The bones are often fragmented and the entirely preserved specimens are relatively rare. Among these, mainly metacarpal and metatarsal bones or phalanges have been preserved completely. Almost all fracture types mentioned by Lyman (1996), except smooth perpendicular one, were recorded on fragments (Fig. 10). In most cases, the bones show irregular perpendicular and/or spiral fractures. The flaking and sawtoothed fractures were the least common. Bone fragmentation

is due to various causes, both abiotic and biotic. Part of the bones have been fragmented during the excavation work. The ancient fragmentation and fractures could be an effect of hunting and/or scavenging by predators, which left bite marks on bones, possibly produced by small felid, canid or mustelid predators (Rodríguez-Hidalgo et al., 2020). An ancient man activity is also not excluded (see below).

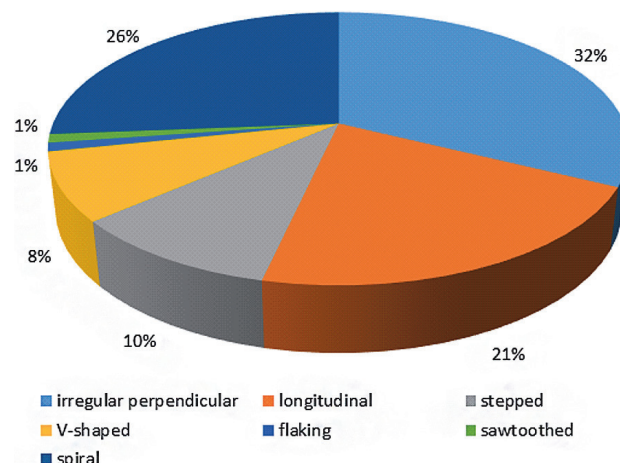


Fig. 10. The percentage of individual fracture types found on bird bones under study from Prepoštská jaskyňa Cave.

5. DISCUSSION

The avifaunal fossil record from the Last Glacial Period is known from several palaeontological as well as archaeological sites of Central Europe. However, many of these faunas are not yet evaluated in detail, or are waiting for a revision. Recently, the Last Glacial bird assemblages of Central Europe have been analyzed in detail mainly from Poland (Bocheński et al., 2012). Biśnik Cave, Komarowa Cave and Deszczowa Cave are the most famous Polish sites with rich avifaunal fossil record (Nadachowski et al., 2009).

Biśnik Cave is very unique due to a fact that it is one of the few sites in Europe, and the only one in Poland, with 300,000-years-long uninterrupted sedimentary sequence which covers the time span from the pre-Saalian to the Holocene (before the Odra Glacial Period to the Holocene) (Tomek et al., 2012). Moreover, a sequence of at least 10 mid-Palaeolithic cultural levels makes Biśnik Cave one of the most important Middle Palaeolithic sites in Central Europe (Cyrek et al., 2010). Bird remains from Biśnik Cave consist of 1,600 skeletal fragments of at least 96 taxa that represent a minimum of 285 individuals (Tomek et al., 2012). However, only 45 bird species are mentioned from the Last Glacial Period (Faunal Complexes II–V). Their diversity is thus only about eight species higher than in Prepoštská jaskyňa Cave (Fig. 11). The recorded species at the Polish site were classified into 5 ecosystem groups: amphibious, forest, ecotone, open and tundra habitat. Some species from these ecosystem groups have also been identified at the Slovak locality (Supplement 2). The main difference is the occurrence of *Loxia curvirostra* (nowadays very rare in Poland), *Arenaria interpres*, *Carduelis flammea*, *Dryocopus martius*, *Alauda arvensis*, *Perdix perdix*, or *Anas strepera* (Tomek et al., 2012) at the Polish site and their absence in the Slovak one.

Komarowa Cave's sedimentary record probably extends to the upper part of the Middle Pleistocene, with 16 layers representing several climatic phases (oscillations) of the Vistulian Glacial Period (Nadachowski et al., 2009). The largest quantity of avifaunal fossils has been found just in these Last Glacial deposits. The bird assemblage diversity was more than a third higher comparing to the avifaunal diversity from Prepoštská jaskyňa Cave (Fig. 11). The difference can be visible especially in comparison of tundra assemblages (Supplement 2). In addition to the *Lagopus lagopus* and *L. muta*, found also in Prepoštská jaskyňa Cave, the tundra assemblage from Komarowa Cave is also represented by *Pluvialis apricaria*, *P. squatarola*, *Arenaria interpres*, *Bubo scandiacus*, *Charadrius cf. morinellus*, *Nyctea scandiaca*, cf. *Eremophila alpestris*, cf. *Calcarius lapponicus*, and *Plectrophenax nivalis* (Nadachowski et al., 2009). A similar situation is also among species living in an open country environment, when both caves coincide only in species *Coturnix coturnix* and *Tachymarpis melba*. Such differences in avian faunas from both caves can be observed also in ecotone, forest, and amphibious environments (Supplement 2).

The sedimentary filling of Deszczowa Cave, 3 to 4 meters thick (Cyrek, 1997), consists of 11 layers (Madeyska, 2000), most of them probably deposited during the period younger than 120 ka (Nadachowski et al., 2009). Most of bird taxa, 45 species, come

from the Last Glacial Period, especially from layer IV dated to MIS 3. The number of identified bird species in these deposits was the same as in Biśnik Cave (Fig. 11), and thus only eight species higher than in Prepoštská jaskyňa Cave. However, the species composition varied considerably between Deszczowa and Prepoštská jaskyňa caves. The similarity of avian assemblages in both caves is only 20 %, whereas between Biśnik and Prepoštská jaskyňa caves is up to 40 %. The common species at Deszczowa and Prepoštská jaskyňa Cave can be found in all environmental groups and include *Lagopus lagopus*, *L. muta*, *Coturnix coturnix*, *Falco tinnunculus*, *Coloeus monedula*, *Lyrurus tetrrix*, *Tetrao urogalus*, *Asio otus*, *Nucifraga caryocatactes*, *Garrulus glandarius*, *Anas platyrhynchos*, *Gallinago gallinago*, *Philomachus pugnax*, and *Asio flammeus* (Supplement 2).

In the territory of Slovakia, Prepoštská jaskyňa Cave can be compared with Lučivnianska Cave 1, also known as Dlhá Diera Cave (Soják et al., 2008). The species composition of avifauna from this Palaeolithic site was much poorer than in Prepoštská jaskyňa Cave, including only nine species (Supplement 2). The cold open landscape – tundra to steppe – is indicated by the occurrence of *Lagopus lagopus*, *L. muta*, and cf. *Anthropoides virgo*. However, the remains of ptarmigans from Lučivnianska Cave 1 have been discovered in younger sediments, probably dated to the Magdalenian (16,000 – 12,400/11,500 BC) or to the younger Świderian culture. The transition from open country to boreal forest is documented by *Pyrrhocorax pyrrhocorax*. The forest landscape is recorded based on *Lyrurus tetrrix*, *Tetrao urogallus*, and *Aquila chrysaetos*, whereas *Anas cf. strepera* and cf. *Philomachus pugnax* indicate an aquatic palaeoenvironment. However, these assemblages already correspond with the beginning of the Holocene. The climate warmed considerably at this time in our territory and the forest vegetation began to spread (Soják et al., 2008).

The comparison of bird diversity among Slovak and Polish sites (Fig. 11) shows not only a difference in number of taxa, but also in the species composition of single avian faunas (Supplement 2). Apart of sampling bias, the main role could play local climatic and environmental conditions. All compared localities are typical caves, while Prepoštská jaskyňa Cave is an

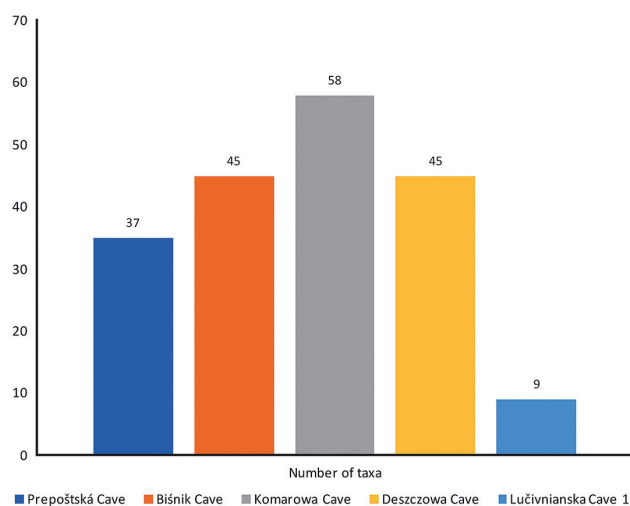


Fig. 11. Comparison of species diversity in compared caves based on the number of taxa.

„abri-like“ cavity in the travertine body, which was formed by a hot mineral spring. The existence and activity of such spring could create a micro-climatic condition suitable for the survival of thermophilous faunal elements from wider areas even during the coldest phases of the Last Glacial. On the other hand, the identified *Lagopus*-assemblage is a typical northern element of Weichselian avifaunas, whose presence in Central Europe was caused by the movement of the continental glacier to the south (Bocheński, 2002).

Generally, it can be assessed that the avifauna from Prepošťská jaskyňa Cave, despite some differences, corresponds in its composition to the bird assemblages typical for the Last Glacial Period from the Central European territory.

The origin of the bird bone accumulations in the locality under study remains questionable. As mentioned above, it can be a result of activity of small carnivores, but it could also be influenced by owls or raptors nesting in or near the cave in the time of the man absence. Some bones also show perforations of regular shape equally arranged one above the other or side by side. This might indicate a human (Neanderthal) activity, but the identification of traces associated with anthropic activity was not the aim of this paper and such considerations are so far only in the hypothetical level. On the other hand, the Neanderthal exploitation of birds is known from several European sites (e.g. Blasco et al., 2016; or Gómez-Olivencia et al., 2018) and there is an assumption that this humankind hunted birds not only for food, but also used their bones (mainly talons) as personal adornments (Romandini et al., 2014; Radovčić et al., 2015, 2020). In addition, Finlayson et al. (2012) demonstrated that the extraction of feathers from birds by Neanderthals was also a temporary and geographically widespread phenomenon and mainly raptors (eagles) and corvids (ravens) were hunted for this purpose (Gómez-Olivencia et al., 2018).

From the viewpoint of Minimum Number of Individuals (MNI, Tab. 1), the most represented bird species in sedimentary filling of Prepošťská jaskyňa Cave are willow ptarmigans (*Lagopus lagopus*), black grouse (*Lyrurus tetrrix*), and rock ptarmigan (*L. muta*). Whether these were hunted by Neanderthals (if ever) only for meat or also for feathers or bones (adornments) remains unknown.

6. CONCLUSION

A detailed taxonomic analysis of bird osteological remains from trenches II and III at the Neanderthal site of Prepošťská jaskyňa Cave shows the presence of 37 species from 11 orders (Anseriformes, Galliformes, Columbiformes, Gruiformes, Charadriiformes, Apodiformes, Accipitriformes, Strigiformes, Falconiformes, Passeriformes, and Coraciiformes). The determined taxa were classified into four main assemblages: northern assemblage with typical species *Lagopus lagopus* and *L. muta*; intermediate or migratory assemblage with index species *Crex crex* and *Gallinula chloropus*; assemblage of cosmopolitan species such as *Anas platyrhynchos* and *Turdus merula*; and thermophilic or southern assemblage with characteristic species *Tachymarptis melba*. Although bird remains are more

or less mixed (mainly in the trench III), at least the northern bird assemblage of the defined ones can be considered as a fossil assemblage from the Last Glacial Period, representing an open land with a cooler climate compared to the prevailing climate in the studied territory at present. The other identified bird assemblages may originate during warmer phases(-s) of the Last Glacial, although their Holocene age is also not fully excluded. The taphonomy of bird remains indicates activity of predators. The human activity was not directly documented, but is not excluded. Almost all Lyman's types of fractures were found, with the predominance of irregular perpendicular, spiral, and longitudinal ones.

Acknowledgements: This work was carried out with financial support from the Slovak Research and Development Agency of the Ministry of Education, Science, Research and Sport of the Slovak Republic (project APVV-16-0121: Geodynamics of the Alpine-Carpathian junction constrained by dating of the Cenozoic evolutionary phases in the Vienna and Danube basins) and the Scientific Grant Agency of the Ministry of Education, Science, Research and Sport of the Slovak Republic (project VEGA 1/0164/19: Biostratigraphy of terrestrial deposits from the Cenozoic Era in the Slovak territory of the Western Carpathians). The authors gratefully acknowledge the helpful comments and constructive suggestions of Z. Bocheński, P. Neruda, and T. Čeklovský for improvement of the manuscript. Their gratitude goes also to Editor J. Schlögl for handling the manuscript and to A. Tutková and A. Domsóvá for English language review.

References

- Bárta J., 1972: Pravek Bojníc. Od staršej doby kamennej po dobu Slovenskú [Prehistory of Bojnice. From the Early Stone Age to the Slavonic Age]. Obzor Publishing, Bratislava, 38 p. [in Slovak]
- Blasco, R., Rosell, J., Rufà, A., Sanches Marco, A. & Finlayson, C., 2016: Pigeons and choughs, a usual resource for the Neanderthals in Gibraltar. *Quaternary International*, 421, 62–77.
- Bocheński, Z., 2002: Bird remains from Oblazowa – zoogeographical and evolutionary remarks. *Acta zoologica cracoviensia*, 45 (special issue), 239–252.
- Bocheński, Z., Bocheński, Z. M. & Tomek, T., 2012: A History of Polish Birds. Institute of Systematics and Evolution of Animals – Polish Academy of Sciences, Kraków, 226 p.
- Cyrek, K., 1997: Ergebnisse der bischeringen Ausgrabungen in der Deszczowa Höhle in Kostkowice, Woiwodschaft Czestochowa. *Badania Archeologiczne na Górnym Śląsku i ziemiach pogranicznych w roku 1994*. Centrum Dziedzictwa Kulturowego Śląska, Katowice, 36–46.
- Cyrek, K., Socha, P., Stefaniak, K., Madeyska, T., Mirosław-Grabowska, J., Sudol, M., and Czyżewski, Ł., 2010: Palaeolithic of Biśnik Cave (Southern Poland) within the environmental background. *Quaternary International*, 220, 5–30.
- Čeklovský T., 2014: Pleistocene horse record from the Neanderthal site of Bojnice I – Prepošťská jaskyňa Cave. *Acta Geologica Slovaca*, 6, 2, 179–189. [in Slovak with English abstract and summary]
- Čeklovský T., 2015: Palaeoenvironment in the territory of Bojnice in the time of the presence of Neanderthals – a model case at Prepošťská jaskyňa Cave site. PhD Thesis, Comenius University in Bratislava, Bratislava, 189 p. [in Slovak with English abstract]

- Čeklovský T., Sabol M., Obuch J., Beňuš R., Bocherens H., Nývltová Fišáková M. & Kováčová M., 2016: Prepoštská jaskyňa Cave – Preliminary results of paleozoological research. *Slovenský kras – Acta Carsologica Slovaca*, 54, 2, 164–192.
- Ellenberger W. & Baum H., 1943: *Handbuch der vergleichenden Anatomie der Haustiere* [Handbook of Comparative Anatomy of Pets]. 18th Edition, Springer-Verlag OHG, Berlin, 1155 p.
- Finlayson, C., Brown, K., Blasco, R., Rosell, J., Negro, J. J., et al., 2012: Birds of a Feather: Neanderthal Exploitation of Raptors and Corvids. *Plos One*, 7, 9, 1–9.
- Goméz-Olivencia, A., Sala, N., Núñez-Lahuerta, C., Arlegi, M. & Rios-Garzaiz, J., 2018: First data of Neanderthal bird and carnivore exploitation in the Cantabrian Region (Axlor; Barandiaran excavations; Dima, Biscay, Northern Iberian Peninsula). *Scientific Reports*, 8, 1–13.
- Hume, R., 2004: *Vtáky Európy* [Birds of Europe]. Ikar, Bratislava, 448 p. [in Slovak]
- Kovalik P., Topercer J., Karaska D., Danko Š. & Šrank V., 2010: Zoznam vtákov Slovenska k 7. 4. 2010 [A list of birds of Slovakia as of April 7, 2010]. *Tichodroma*, 22, 97–108. [in Slovak]
- Lyman L. R., 1996: *Vertebrate Taphonomy*. Cambridge University Press, Cambridge, 524 p.
- Ložek V., 1962: Aké zmeny prekonala príroda Hornej Nitry v najmladšej geologickej minulosti [What changes did the nature of Horná Nitra overcome in the youngest geological past]. *Horná Nitra* (Vlastivedný zborník), 1, 203–228. [in Slovak]
- Madeyska, T., 2000: Sediments and stratigraphy. In: Cyrek, K., Nadachowski, A., Madeyska, T., Bocheński, Z., Tomek, T., Wojtal, P., Miękina, B., Lipecki, G., Garapich, A., Rzebik-Kowalska, B., Stworzewicz, E., Wolsan, M., Godawa, J., Kościów, R., Fostowicz-Frelik, L & Szyndlar, Z. (Authors): Excavation in the Deszczowa Cave (Kroczyckie Rocks, Czestochowa Upland, Central Poland). *Folia Quaternaria*, 71, 11 – 17.
- Marcus L. F., 1990: Chapter 4. Traditional morphometrics. In: Rohlf F. J. & Bookstein F. L. (Eds.): *Proceedings of the Michigan Morphometric Workshop*. Special Publication No. 2. Ann Arbor MI, The University of Michigan Museum of Zoology, Michigan, pp. 77–122.
- Medvecký K. A., 1927: Paleolitická jaskyňa v Bojniciach [A Palaeolithic cave in Bojnice]. *Sborník Muzeálnej slovenskej spoločnosti*, 21, 109–111. [in Slovak]
- Mlíkovský J., 1996: Tertiary Avian Faunas of Europe. *Acta Universitatis Carolinae, Geologica*, 39, 777–818.
- Mlíkovský J., 2002: *Cenozoic Birds of the World. Part 1: Europe*. Ninox Press, Prague, 417 p.
- Nadachowski, A., Zarski, M., Urbanowski, M., Wojtal, P., Miękina, B., Lipecki, G., Ochman, K., Krawczyk, M., Jakubowski G. & Tomek, T., 2009: Late Pleistocene Environment of the Czestochowa Upland (Poland) Reconstructed on the Basis of Faunistic Evidence from Archeological Cave Sites. Institute of Systematics and Evolution of Animals, Polish Academy of Science, Kraków, 112 p.
- Neruda P. & Kaminská L., 2013: Neanderthals at Bojnice in the context of Central Europe. *Anthropos, Studies in Anthropology, Palaeoethnology, Palaeontology and Quaternary Geology*, 36, N.S. 28, 248 p.
- Popesko P., 1992: *Anatómia hospodárskych zvierat* [Livestock Anatomy]. Príroda, Bratislava, 693 p. [in Slovak]
- Prošek F., 1952: Výzkum Prepoštské jeskyně v Bojnicih r. 1950 [Research of Prepoštská jaskyňa Cave in Bojnice in 1950]. *Archeologické rozhledy*, 4, 3–9. [in Czech]
- Prošek, F. & Ložek, V., 1951: Zpráva výskumu kvartéru paleolitického sídliště v Bojnicih [Research report of the Quaternary of the Palaeolithic settlement in Bojnice]. *Věstník ÚÚG*, 26, Praha, 104–107. [in Czech]
- Radovčić, D., Birarda, G., Oros Sršen, A., Vaccari, L., Radovčić & Frayer, D. W., 2020: Surface analysis of an eagle talon from Krapina. *Scientific Reports*, 10, 6329.
- Radovčić, D., Oros Sršen, A., Radovčić, J., Frayer, D. W. & Petraglia, M. D., 2015: Evidence for Neanderthal Jewelry: Modified White-Tailed Eagle Claws at Krapina. *PLoS One*, 10, 3, e0119802.
- Rodríguez-Hidalgo, A., Sanz, M., Daura, J. & Sánchez-Marco, A., 2020: Taphonomic criteria for identifying Iberian lynx dens in Quaternary deposits. *Scientific Reports*, 10, 7225. <https://doi.org/10.1038/s41598-020-63908-6>
- Romandini, M., Peresani, M., Laroulandie, V., Metz, L., Pastoors, A., Vaquero, M. & Slimak, L., 2014: Convergent Evidence of Eagle Talons Used by Late Neanderthals in Europe: A Further Assessment on Symbolism. *Plos One*, 9, 7, e101278.
- Soják, M., Obuch, J. & Holec, P., 2008: Osteologický materiál vtákov a cicavcov (Vertebrata – Aves et Mammalia) z archeologického výskumu Lučivnianskej jaskyne [Osteological material of birds and mammals (Vertebrata – Aves et Mammalia) from archaeological research of the Lučivnianska Cave]. *Študijné zvesti archeologického ústavu SAV*, 43, Nitra, 235–249. [in Slovak]
- Šedivá M., 2016: *Kenozoická avifauna Slovenska* [Cenozoic avifauna of Slovakia]. Bachelor Thesis, Comenius University in Bratislava, Bratislava, 82 p. [in Slovak with English abstract]
- Šedivá M., 2018: *Avifauna z neandertálskej lokality Prepoštská jaskyňa* [Avifauna from the Neanderthal site of Prepoštská jaskyňa Cave]. Diploma Thesis, Comenius University in Bratislava, Bratislava, 193 p. [in Slovak with English abstract]
- Tomek, T., Bocheński, Z. M., Socha, P. & Stefaniak, K., 2012: Continuous 300,000-year fossil record: changes in the ornithofauna of Biśnik Cave, Poland. *Palaeontologia Electronica*, 15, 1, 2A: 20 p.

Supplement 1. Systematic palaeontology of determined bird taxa from Prepoštská jaskyňa Cave.

Supplement 2: Comparison of the Last Glacial bird species diversity in individual mentioned caves (data source: Soják et al., 2008; Nadachowski et al. 2009; Tomek et al., 2012).