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Weichselian and Holocene bird remains from Komarowa Cave, Central Poland

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Abstract. Identified bird remains from Komarowa Cave consist of 1872 skeletal fragments of at least 106 taxa. They come from sediments accumulated between the Early Glacial and Holocene, and represent various habitats of all European climatic zones. The most interesting are the fairly numerous bones of the Alpine Swift indicating the presence of a breeding colony far from its recent breeding range. Ten bird taxa are new for the Polish Pleistocene avifauna.

Key words: fossil birds, Komarowa Cave, Central Poland, Weichselian, Holocene.

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I. INTRODUCTION

Komarowa Cave is situated ca 10 km south to south-east of Częstochowa, in the northern part of the Częstochowa Uplands (Fig. 1). Its entrance is on the northern slope of Puchacz Hill, about 340 m a.s.l. and 30-40 m above the valley bottom. Excavations, both inside the cave and at the terrace in front of its entrance, took place between 1997-2001. At first they were directed by Dr M. ŻARSKI of the Geological Institute, and then by Dr M. URBANOWSKI of Warsaw University. In the final years, members of the staff of the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences in Kraków also took part in the excavations. A full geological and sedimentological description of particular layers of sediment was published by ŻARSKI (2005). Not all layers distinguished inside the cave correspond with those from the terrace, but altogether they are complementary (Fig. 2). Generally they give a fairly good picture of habitat and faunal changes during the whole period of sediment accumulation. Excavated bird remains are stored in the collection of the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences in Kraków.

Ten samples from various layers of sediment were dated using the radiocarbon (14C) method, and seven using the Termoluminiscence (TL) method. The former dates range from 46100±900 BP to 24550±220 BP whereas the TL dates are between 16700±2000 BP and 9900±1300 BP (ŻARSKI 2005). In most cases the dates agree with the sequence of layers, and only those from the lower part of the uppermost layers A and A' (41700 BP, 42200 BP, 46100BP) indicate disturbance of sedi-

Fig. 1. Localization of Komarowa Cave.

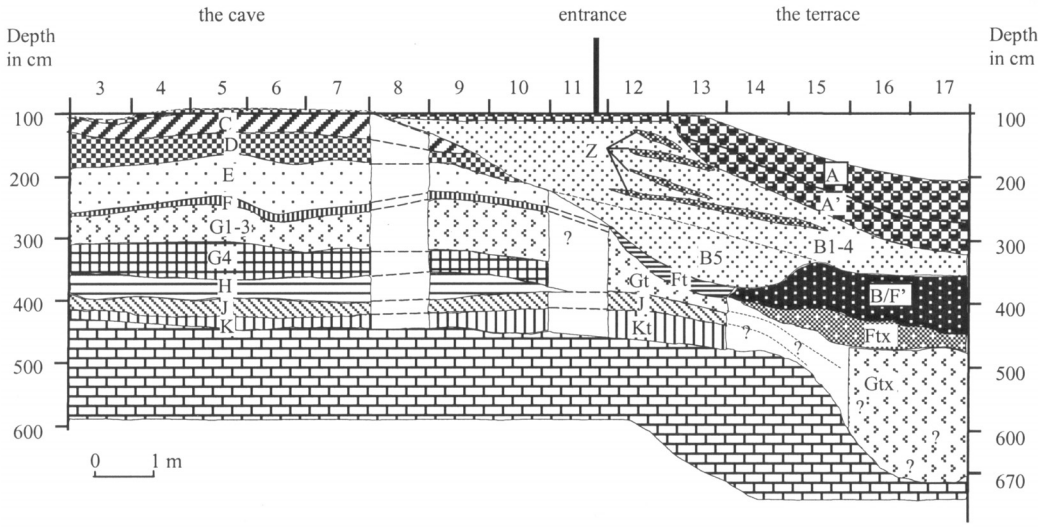

Fig. 2. Longitudinal profile of the sediment in Komarowa Cave (after ŻARSKI 2005).

ments. Sediments older than those of the Middle Weichselian (OIS 3) layer E were dated indirectly. However, from the viewpoint of the fossil bird fauna they are not very important because bird remains from the deepest layers are not numerous.

II. MATERIAL AND METHODS

Bird remains from the excavations in Komarowa Cave consist of 1872 skeletal fragments of at least 106 taxa, identified in most cases to species level. Additionally there were many small bone fragments and elements such as foot phalanges or vertebrae of small birds which remain unidentified. Of the above mentioned 1872 fragments, 42 belonging to at least 15 species have no defined stratigraphy, however all of them represent taxa known from well defined layers, so we have left them without comments.

1059 identified bone fragments were found in sediments excavated inside the cave, and another 771 came from the terrace in front of it. Altogether they represent at least 416 individuals. The identified remains excavated inside the cave are summarized in Table I and those from the terrace in Table II. The numbers of specimens and the minimum numbers of individuals are usually given in both tables. The MNI was not given in the cases of imprecisely identified fragments because they may belong to unequivocally identified species recorded in the same layer. The degree of ossification of some bones summarized in Tables I and II indicates that these belonged to juvenile and immature birds – they are numbered in Table III. In particular, the presence of not fully developed bones of juveniles indicates that they must have nested within a radius of several kilometers from the cave, i.e. the maximum hunting range of an owl nesting in the cave.

Table I

Bird remains identified in particular layers inside Komarowa Cave. The first number in the column refers to the number of identified skeletal fragments (NISP), the second refers to the minimum number of individuals (MNI) in a given layer. MNI is not given in the case, when remains may belong to individuals identified to species level or to specimens coming from transitional sediments between layers in which given species was found. Numbers written in italics added in the column concerns specimens not surely identified (in some cases juveniles or subadult individuals)

Species	Layer										Total
	H	G4	G	F	E	D	C	A	B/D	D/E	
Podiceps auritus (LINNAEUS, 1758) / *nigricollis* C. L. BREHM, 1831						1/1					1/1
Anas platyrhynchos LINNAEUS, 1758					1/1	6/2 *+1*					7/3 *+1*
Anas querquedula LINNAEUS, 1758					1/1	1/1					2/2
Anas querquedula/A.*crecca* LINNAEUS, 1758			1/1								1/1
cf. *Mergellus albellus* (LINNAEUS, 1758)					1/1						1/1
Anatidae (middle sized duck)					1						1
Buteo sp.						1/1					1/1
Aquila chrysaetos (LINNAEUS, 1758)						1/1	1/1				2/2
Accipitridae (size of *Aquila clanga, pomarina*)					1/1						1/1
Falco tinnunculus LINNAEUS, 1758					3/1	3/2					6/3
Falco columbarius LINNAEUS, 1758					1/1						1/1
Falco subbuteo LINNAEUS, 1758					1/1	1/1					2/2
Falco cherrug J. E. GRAY, 1834						1/1					1/1
Falco peregrinus TUNSTALL, 1771			1/1			1/1	1/1				3/3

Species	Layer										Total
	H	G4	G	F	E	D	C	A	B/D	D/E	
Falco sp.					1	2	2				5
Lagopus lagopus (LINNAEUS, 1758)			1/1	2/1	152/13	139/17	6/1		2/1		302/34
Lagopus muta (MONTIN, 1781)						3/1					3/1
Lagopus lagopus /muta					33	24					57
Tetrao tetrix LINNAEUS, 1758	1/1	1/1	2/1		76/6	96/6	7/1				183/16
Tetrao urogallus LINNAEUS, 1758	1/1				4/1	2/1	7/1				14/4
Tetrao sp.					2			1			3
Perdix perdix (LINNAEUS, 1758)						1/1					1/1
Coturnix coturnix (LINNAEUS, 1758)						1/1					1/1
Galliformes indet.					8	15					23
Rallus aquaticus LINNAEUS, 1758						2/1					2/1
Crex crex (LINNAEUS, 1758)						1/1					1/1
Porzana porzana (LINNAEUS, 1766)						1/1					1/1
Gallinula chloropus (LINNAEUS,1758)						1/1					1/1
Tetrax tetrax (LINNAEUS, 1758)					1/1	1/1					2/2
Vanellus vanellus (LINNAEUS, 1758)						1/1					1/1
Pluvialis apricaria (LINNAEUS, 1758)					1/1	2/1					3/2
Pluvialis squatarola (LINNAEUS, 1758)						1/1	1/1				2/2
Charadrius cf. *morinellus* (LINNAEUS, 1758)					1/1					1	2/1
Charadrius sp.					1						1
Gallinago media (LATHAM 1787)					1/1	2/1					3/2
Galinago gallinago (LINNAEUS, 1758)					1/1						1/1
Arenaria interpres (LINNAEUS, 1758)					1/1	*1/1*					1/1 *+1/1*
Philomachus pugnax (LINNAEUS, 1758)					1/1						1/1
Columba palumbus LINNAEUS, 1758						1/1					1/1
Bubo bubo (LINNAEUS, 1758)					1/1						1/1
Nyctea scandiaca (LINNAEUS, 1758)							1/1 *+1/1*				1/1 *+1/1*
cf. *Strix uralensis* PALLAS, 1771						1/1					1/1
Tachymarptis melba (LINNAEUS, 1758)					13/3	10/2	2/2				25/7
cf. *Galerida cristata* (LINNAEUS, 1758)						5/2					5/2
Lullula arborea (LINNAEUS, 1758)					*2/1*	7/1 *+1*					7/1 *+3/1*
Alauda arvensis LINNAEUS, 1758				1/1	19/4 *+4*	34/4 *+2*					54/9 *+6*
cf. *Eremophila alpestris* (LINNAEUS 1758)						1/1					1/1
Alaudidae indet.					2	3					5
Hirundo rustica LINNAEUS, 1758			1/1		4/2	9/3					14/6

Species	Layer										Total
	H	G4	G	F	E	D	C	A	B/D	D/E	
Delichon urbicum (LINNAEUS, 1758)				1/1	1/1						2/2
cf. *Motacilla alba* LINNAEUS, 1758					1/1						1/1
Anthus pratensis (LINNAEUS, 1758)						1/1					1/1
Anthus cf. *trivialis* (LINNAEUS, 1758)						1/1					1/1
Lanius excubitor LINNAEUS, 1758					1/1	*1/1*					1/1 *+1/1*
Phoenicurus sp.						1/1					1/1
Oenanthe oenanthe (LINNAEUS, 1758)					2/1	3/1			*1/1*		5/2 *+1/1*
cf. *Monticola saxatilis* (LINNAEUS, 1766)						1/1					1/1
Turdus merula LINNAEUS, 1758					2/1	12/4					14/5
Turdus pilaris LINNAEUS, 1758					2/1	9/2					11/3
Turdus cf. *iliacus* LINNAEUS, 1766					1/1						1/1
Turdus philomelos C. L. BREHM, 1831					6/2 *+5/1*	22/4 *+4*					28/6 *+9/1*
Turdus viscivorus LINNAEUS, 1758			1/1			4/2	2/1				7/4
Turdus sp.					12	15	1				28
Turdidae						1					1
Ficedula hypoleuca (PALLAS, 1764)						1/1					1/1
Sitta europaea LINNAEUS, 1758					1/1 *+1*	1/1					2/2 *+1*
Emberiza citrinella LINNAEUS, 1758					3/1	5/1 *+2*					8/2 *+2*
cf. *Calcarius lapponicus* (LINNAEUS, 1758)						1/1		1/1			2/2
cf. *Plectrophenax nivalis* (LINNAEUS, 1758)					1/1	2/1					3/2
Fringilla cf. *coelebs* LINNAEUS, 1758			1/1			1/1					2/2
Carduelis chloris (LINNAEUS, 1758)					2/1	*5/2*					2/1 *+5/2*
Carduelis carduelis (LINNAEUS, 1758)						1/1					1/1
Loxia cf. *curvirostra* LINNAEUS, 1758			1/1			2/1		1/1			4/3
Loxia sp.						5/2					5/2
cf. *Pyrrhula pyrrhula* (LINNAEUS, 1758)						3/1					3/1
Coccothraustes coccothraustes LINNAEUS, 1758						3/1 *+3*					3/1 *+3*
Montifringilla nivalis (LINNAEUS, 1766)					1/1	5/3					6/4
Sturnus vulgaris LINNAEUS, 1758				2/1	18/4 *+3*	26/3					46/8 *+3*
Oriolus oriolus (LINNAEUS, 1758)						1/1					1/1
Garrulus glandarius (LINNAEUS, 1758)					4/1						4/1
cf. *Pyrrhocorax graculus* (LINNAEUS, 1766)					1/1						1/1
Corvus monedula LINNAEUS, 1758					16/3	25/3	1/1				42/7

Species	Layer										Total
	H	G4	G	F	E	D	C	A	B/D	D/E	
Corvus corax LINNAEUS, 1758					3/1	8/2					11/3
Corvidae (small)					3	3					6
Passeriformes indet					5	3					8
Total NISP	2	1	9	6	434	567	33	3	3	1	1059
Total MNI	2	1	8	4	70	107	12	2	2		208
Total number of taxa	2	1	7	4	42	58	11	2			72

Table II

Bird remains identified in particular layers of the terrace in front of Komarowa Cave. All explanations as in Table I

Species	Layer									Total
	Gtx	Ft	B/F'	Z	B5	B	A/B	A'	A	
Branta leucopsis (BECHSTEIN, 1803)			1/1			1/1				2/2
Branta bernicla (LINNAEUS, 1758)						1/1				1/1
Anas platyrhynchos LINNAEUS, 1758			2/2			4/1 *+1*			1/1 *+1*	7/4 *+2*
Anas querquedula LINNAEUS, 1758 / A. *crecca* LINNAEUS, 1758						1/1				1/1
cf. *Aythya marila* (LINNAEUS, 1761)			1/1							1/1
Aquila chrysaetos (LINNAEUS, 1758)							1/1			1/1
Falco subbuteo LINNAEUS, 1758									1/1	1/1
Falco cherrug J. E. GRAY, 1834						1/1				1/1
Falco cherrug / F.rusticolus			2/1			1/1				3/2
Falco rusticolus LINNAEUS, 1758			1/1			6/1				7/2
Falco sp.						1				1
Lagopus lagopus (LINNAEUS, 1758)		2/1	56/12	32/8	10/4	142/18	2/1	1/1	35/6	280/51
Lagopus muta (MONTIN, 1781)		1/1	2/1			4/1			4/1	11/4
Lagopus lagopus/muta			8	2	2	35			6	54
Tetrao tetrix LINNAEUS, 1758			5/2	2/1	1/1	35/4			11/2	54/10
Tetrao urogallus LINNAEUS, 1758				2/1		6/1			8/2	16/4
Tetrao sp.						1				1
Bonasa bonasia (LINNAEUS, 1758)									1/1	1/1
Perdix perdix (LINNAEUS, 1758)									1/1	1/1
Gallus gallus (LINNAEUS, 1758)									2/2	2/2

Species	Layer									Total
	Gtx	Ft	B/F'	Z	B5	B	A/B	A'	A	
Galliformes indet.				1	2	6			3	12
Porzana porzana (LINNAEUS, 1766)						1/1				1/1
Fulica atra LINNAEUS, 1758			1/1			1/1			1/1	3/3
Vanellus vanellus (LINNAEUS, 1758)			1/1							1/1
Pluvialis apricaria (LINNAEUS, 1758) / *P. fulva* J. F. GMELIN,1789			1/1			1/1				2/2
Pluvialis squatarola (LINNAEUS, 1758)			1/1			1/1				2/2
Charadrius cf. *dubius* SCOPOLI, 1786						1/1				1/1
Charadrius cf. *morinellus* (LINNAEUS, 1758)						1/1				1/1
Lymnocryptes minimus (BRÜNICH, 1764)				*1/1*		3/3				3/3 *+1/1*
Gallinago media (LATHAM, 1787)						2/1			1/1	3/2
Gallinago gallinago (LINNAEUS, 1758)									2/1	2/1
Limosa limosa (LINNAEUS, 1758)						1/1				1/1
Limosa lapponica (LINNAEUS, 1758)									1/1	1/1
Numenius sp.									1/1	1/1
Arenaria interpres (LINNAEUS, 1758)						1/1			*1/1*	1/1 *+1/1*
Philomachus pugnax (LINNAEUS, 1758)						1/1			1/1 *+1*	2/2 *+1*
Tringa erythropus (PALLAS, 1764)				1/1						1/1
Tringa totanus (LINNAEUS, 1758)						1/1				1/1
Tringa cf. *nebularia* (GUNNERUS, 1767)						1/1				1/1
Actitis hypoleucos (LINNAEUS, 1758)				1/1						1/1
Larus ridibundus LINNAEUS 1766						1/1				1/1
Charadriiformes indet (size of *T. nebularia)*						1				1
Columba oenas LINNAEUS, 1758									2/1	2/1
Cuculus canorus LINNAEUS, 1758									1/1	1/1
Glaucidium passerinum (LINNAEUS, 1758)								2/1		2/1
Caprimulgus europaeus LINNAEUS, 1758						1/1			*1/1*	1/1 *+1/1*
Dendrocopos major (LINNAEUS, 1758)	1/1								8/2	9/3
Dryocopus martius (LINNAEUS, 1758)									2/2	2/2
Picus canus J.F. GMELIN, 1788						1/1			1/1	2/2
Piciformes indet						1				1
cf. *Calandrella cinerea* J. F. GMELIN 1789									1/1	1/1
Lullula arborea (LINNAEUS, 1758)					2/1				1/1 *+1*	3/2 *+1*

Species	Layer									Total
	Gtx	Ft	B/F'	Z	B5	B	A/B	A'	A	
Alauda arvensis LINNAEUS, 1758				*1/1*		2/1			3/1	5/2 *+1/1*
Hirundo rustica LINNAEUS, 1758						2/1			1/1	3/2
Anthus cf. *pratensis* (LINNAEUS, 1758)						1/1			1/1	2/2
Anthus sp.									1/1	1/1
Erithacus rubecula LINNAEUS, 1758						1/1				1/1
Phoenicurus sp.						1/1				1/1
Oenanthe oenanthe (LINNAEUS, 1758)			*1/1*			1/1				1/1 *+1/1*
Turdus merula LINNAEUS, 1758						3/2		4/2	13/2	20/6
Turdus pilaris LINNAEUS, 1758						5/2 *+1*		5/1	21/6 *+3*	31/9 *+4*
Turdus cf. *iliacus* LINNAEUS, 1766									1/1	1/1
Turdus philomelos C. L. BREHM, 1831								1/1	8/2 *+1*	9/3 *+1*
Turdus viscivorus LINNAEUS, 1758						1/1		*1/1*	26/4 *+5*	27/5 *+6/1*
Turdus sp.	1/1					1			38/2	39/3
Parus major LINNAEUS, 1758									3/1	3/1
Parus caeruleus LINNAEUS, 1758									1/1	1/1
Sitta europaea LINNAEUS, 1758									7/2	7/2
Phylloscopus cf. *collybita* (VIEILLOT, 1817)								1/1	1/1	2/2
Phylloscopus sp.									1/1	1/1
Muscicapa striata (PALLAS, 1764)									1/1	1/1
Emberiza citrinella LINNAEUS, 1758						2/1 *+1*			1/1	3/2 *+1*
Fringilla coelebs LINNAEUS, 1758									5/2 *+2*	5/2 *+2*
Carduelis chloris (LINNAEUS, 1758)						1/1			2/1	3/2
Carduelis cf. *carduelis* (LINNAEUS, 1758)					1/1					1/1
Coccothraustes coccothraustes LINNAEUS, 1758						1/1 *+1*			8/3 *+2*	9/4 *+3*
Fringillidae size of *C. chloris*						1/1				1/1
Montifringilla nivalis (LINNAEUS, 1766)						2/1			1/1	3/2
Sturnus vulgaris LINNAEUS, 1758									7/2 *+1*	7/2 *+1*
Garrulus glandarius (LINNAEUS, 1758)									15/3	15/3
Pica pica (LINNAEUS, 1758)						1/1				1/1
Corvus monedula LINNAEUS, 1758		1/1	1/1		2/1	6/1	2/1			12/5

Species	Layer									Total
	Gtx	Ft	B/F'	Z	B5	B	A/B	A'	A	
Corvus corone LINNAEUS, 1758									1/1	1/1
Corvidae (small)			1			4			3	7
Passeriformes indet			1						5	6
Total NISP	2	4	86	43	20	306	5	15	290	771
Total MNI	2	3	27	14	8	67	3	8	76	208
Total number of taxa	2	3	14	7	5	42	3	7	47	72

The bird assemblages coming from well defined and often dated layers were used for palaeoecological comments concerning habitats and climates in the surroundings of the cave in consecutive periods of time. For this purpose we tried to assign every taxon to one of four groups of habitats, distinguished on the basis of the breeding requirements: "forest", "water-and-marsh", "open habitats", and "rocks". The "forest" habitats comprised all types of forests, and also parklands, shrubs, and even single trees if they are necessary for breeding of particular species. "Water-and-marsh" habitats contain all types of freshwater lakes, ponds, rivers, marshes and even wet meadows, and sometimes also sea coasts, if humidity is required by birds. The "open habitats" included treeless and dry tundra, meadows, and steppes, irrespective of climatic conditions. In the category "rocks" we included rock crevices, and ledges, and also rubble. However, the grouping of some species in even general habitat types is not always unequivocally possible, because their breeding habitat may fall into two groups. In such cases it was done authoritatively. For example, the commonest among remains, the Willow Grouse, which lives in the Arctic tundra and Boreal forests was included in forest species (because the area of forests seems to be at least equal to that of the area of tundra inhabited by this species in the Western Palaearctic). For characterizing the climate we used the approximate temperatures proposed by LORENC (2004) on the basis of thermic indices calculated according to DEMARCQ and MOURER-CHAUVIRÉ (1976). To minimize random errors in characterizing habitats and climate, only layers providing more than ten taxa were analyzed.

Table III

Skeletal fragments of juvenile (bold font) and subadult (plain font) birds identified in particular layers inside and in front of Komarowa Cave (treated together). Numbers written in italics concern specimens ambiguously identified

Species	Layer								Total
	H	B/F'	E	D	C	Z	B, B5	A, A'	
Anas platyrhynchos		2							2
Mergellus albellus			*1*						*1*
Falco cherrug / F. rusticolus							1		1
Falco rusticolus		1					1		2
Falco sp.					1				1
Lagopus lagopus		9	2			3	**1,** 3	**2**	**3,** 17

Species	Layer								Total
	H	B/F'	E	D	C	Z	B, B5	A, A'	
Lagopus muta							**1**	1	**1** 1
Lagopus lagopus/ muta			1						1
Tetrao tetrix	1		2	1			**1,** 3		**1,** 7
Tetrao urogallus								**1**	**1**
Galliformes indet.			**2**						**2**
Fulica atra		1					1	1	3
Crex crex				1					1
Charadrius sp.			1						1
Gallinago media				1					1
Gallinago gallinago								2	2
Tringa cf. *nebularia*							1		1
Arenaria interpres				*1*					*1*
Alauda arvensis			2						2
Motacilla alba			*1*						*1*
Erithacus rubecula							1		1
Lanius excubitor			1						1
Turdus pilaris								4	4
Turdus philomelos				1 ***1***, *1*					1 ***1***, *1*
Turdus viscivorus								1	1
Turdus sp.			**1,** 3	**2,** 6			1	**3,** 1	**6,** 11
Ficedula hypoleuca				1					1
Sitta europaea								1	1
Emberiza citrinella				*1*			***1***		***1,*** *1*
Coccothraustes coccothraustes							**1**	1	**1** 1
Carduelis chloris				***1***					***1***
Sturnus vulgaris			3 ***1***, *2*	3					6 ***1***, *2*
Pyrrhocorax graculus			*1*						*1*
Garrulus glandarius								1	1
Corvus monedula		1	2	1		**1**	**3,** 5		**3,** 10
Corvidae (small)		**1**	2	1			**1,** 3	3	**2,** 9
Passeriformes indet			**1,** 1	1					**1,** 2
Total NISP	1	**1,** 14	**5,** 25	**4,** 20	1	**1,** 3	**9,** 16	**6,** 16	**26,** 96
Total of taxa	1	**1,** 5	**2,** 15	**3,** 16	1	**1,** 1	**7,** 11	**3,** 11	**11,** 31

III. COMMENTS AND DISCUSSION

A. New taxa for the Polish fossil avifauna

1. The Slavonian or Black-necked Grebe *Podiceps auritus*/*nigricollis* – Only the distal part of a tibiotarsus was identified in layer D in the cave; four radiocarbon dates (ca 35500 to 28500 BP) indicate its deposition during the Denekamp Interstadial of the Interpleniglacial (OIS 3). However, neither morphological nor metric characters discriminating these two grebe species occur in this part of the bone (BOCHEŃSKI Z. M. 1994). Both species breed on fresh water ponds with rich vegetation. Their recent breeding distribution in Europe is complementary (Slavonian Grebe in the Boreal zone, whereas Black-necked Grebe in the Temperate and Warm Temperate Zones), and in Asia their ranges partly overlap. Therefore, their presence indicates the habitat only, and not the climate. According to TYRBERG (1998, 2003) both species have been recorded since the Early Pleistocene.

2. The Saker Falcon *Falco cherrug* – Unequivocally determined remains come from Interpleniglacial layer D in the cave (proximal part of right femur), and layer B on the terrace accumulated between 16700 and 9900 BP (shaft of left femur). According to HARRISON (1982) this species breeds in SE Europe and in Asia "in Temperate to Warm Temperate zones ... in open areas, areas with scattered trees, open forest on plains, steppes, montane plateaus up to 3500 m"; its nearest breeding sites are in Slovakia and Hungary. Ambiguously identified remains of the Saker Falcon are known in Europe from the Early Pleistocene of Romania and the Middle Pleistocene of the Czech Republic; Late Pleistocene remains are more numerous especially in Russia (TYRBERG 1998, 2003).

3. The Little Ringed Plover *Charadrius* cf. *dubius* – The distal part of the left tarsometatarsus was found in layer B on the terrace dated to the last six thousand years of the Pleistocene. It is widely distributed in the Palaearctic from the Boreal to Warm Temperate zones breeding on bare shores of rivers or lakes and similar unvegetated habitats (HARRISON 1982). Fossil remains are listed by TYRBERG (1998) from two localities only: the Middle Pleistocene in France, and Late Pleistocene in Spain.

4. The Bar-tailed Godwit *Limosa lapponica* – A nearly complete left ulna (with only the proximal articular part missing) was found in layer A of the terrace sediment dated to the Holocene. The bone was compared with seven bones of the recent *L. limosa* and two of *lapponica*. The general size of the fossil is similar to those of the latter and to the smallest of *limosa*. The most conspicuous discriminative character seems to be the distances between the feather papillae which in *lapponica* are smaller. According to HARRISON (1982) the Bar-tailed Godwit breeds in the Arctic zone in northern Scandinavia and northern European and Asiatic Russia, in marshy habitats from moss and shrub tundra to the Boreal conifer forest zone in the southern limits of its distribution. Fossil records are only two: Binagady on the western Caspian shore (imprecisely defined age: Middle-Late Pleistocene), and Chudleigh Cave in England (TYRBERG 1998, 2003).

5. The Greenshank *Tringa* cf. *nebularia* – the proximal part of a right carpometacarpus of an immature bird was found in layer B of the terrace sediment accumulated in the Upper Pleniglacial and Late Glacial. Its size points to the largest *Tringa*. The Greenshank breeds in the Boreal zone of Scandinavia and Russia in various biotopes where at least some trees are present (HARRISON 1982). According to TYRBERG (1998) it is known since the Middle Pleistocene of France and Azerbaijan, and from several Late Pleistocene localities widely dispersed in Europe.

6. The Short-toed Lark (?) *Calandrella* sp. (cf. *brachydactyla*) – The proximal part of the right carpometacarpus was found in the Holocene layer A of the terrace. It was compared with two Algerian specimens of *C. rufescens* and one of *brachydactyla* from the Caspian region but not with the Asiatic species *acutirostris* and *raytal*. Its morphology is more similar to *brachydactyla* than to *rufescens*, but there are a few characters separating it from both of them. However the scale of differences between the two studied specimens of *rufescens* indicates the possibility of high individual variation, so without studying a larger series of specimens more precise identification is impossible. The Short-toed Lark breeds in the Mediterranean countries and in Asia in Warm Temperate to Sub-

tropical zones in open steppes, semi-deserts with shrubs and so on (HARRISON 1982). TYRBERG (1998), repeating the data from older papers, cites fossil "*brachydactyla*" from a few south European localities since the Middle Pleistocene and "*cinerea*" from the Ukraine, China and Spain treating them as separate species. They are separate species, but according to CRAMP (1988), HOWARD & MOORE (1991), and del HOYO et al. (2004) this is the breeding area of *brachydactyla*, whereas the Red-capped Lark *C. cinerea* lives in Subsaharan Africa only. However some earlier authors treated these taxa as conspecific, using the species name *brachydactyla* (HARTERT 1904) or *cinerea* (STEGMAN 1938, DEMENTIEV and GLADKOV 1954, VAURIE 1959, HARRISON 1982).

7. The Meadow Pipit *Anthus pratensis* – A complete right humerus was found in layer B and the distal part of a left one in layer A of the terrace sediments; the oldest is a distal part of a right carpometacarpus (ambiguously identified) from layer D in the cave. So, the Meadow Pipit is known since the Interpleniglacial. According to HARRISON (1982) it breeds in the Arctic to Temperate zones of Europe and NW Asia in various habitats, mainly open, but also in open forest, and shrub tundra. Fossil remains are known since the Early Pleistocene of Israel and Spain, two Middle Pleistocene sites in France, and 16 Late Pleistocene sites in several western Palaearctic countries (TYRBERG 1998, 2003), of which the Spanish and two Israeli records are situated outside the recent breeding range.

8. *Phylloscopus* sp. (cf. *collybita*?) – Two bones were found in the Holocene sediments of the terrace (layer A: complete right humerus, and layer A': distal part of right humerus). Both bones are very similar to small bones of the Chiffchaff. However, the size variation of the humerus in the genus *Phylloscopus* is great and overlaps in several species, which indicates that besides the Chiffchaff the bones could belong to *Ph. trochilus* and *inornatus*. Some Asiatic vagrants also cannot be excluded. Of the compared species we can exclude *sibilatrix* and *trochiloides* because of their size (Fig. 3). According to HARRISON (1982) the Chiffchaff breeds in nearly all of Europe, excluding the southern part of Scandinavia, part of Spain, Greece, and part of Ukraine, in Boreal to Warm Temperate zones, in open well grown forest, parkland, in mountains also in bushy mountain

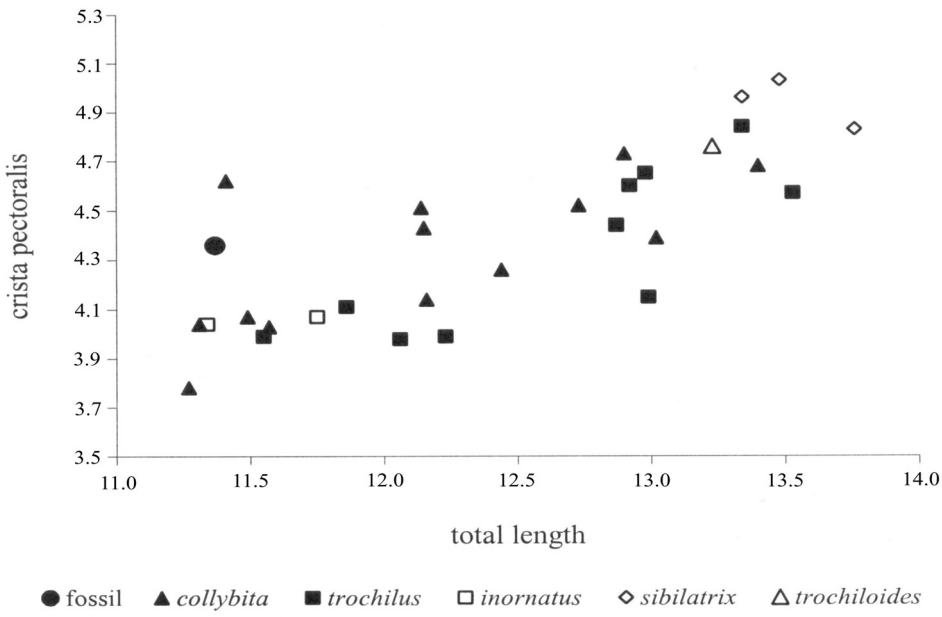

Fig. 3. The ratio of the total length (in mm) of the humerus to the distance between the top of head and distal end of crista pectoralis in fossil and recent Leaf Warblers.

scrub-like dwarf pine. TYRBERG (1998, 2003) mentions it from three Late Pleistocene localities only, however fossils not exactly identified (like *collybita*/*trochilus* or *sibilatrix*/*collybita*) are known from a few other sites - the earliest from the Middle Pleistocene of Italy.

9. The Lapland Bunting (ambiguous identification) cf. *Calcarius lapponicus*. Two fragments found in the cave, in Holocene layer A, left wing phalanx, and in Interpleniglacial layer D, maxillare. It is a typical Arctic bird breeding in moss or shrub tundra of Scandinavia and Russia (HARRISON 1982). TYRBERG (1998) lists this species from two Late Pleistocene sites only i.e. from Zwerglloch in Austria and Chudleigh Cave in England, and stresses that in both cases the sediments accumulated in the Late Pleistocene contain admixture of Holocene materials, which may indicate the late colonization of the Palaearctic by this representative of a typical Nearctic genus. The specimen in layer D suggests that the colonization took place much earlier.

10. The Snow Bunting (ambiguous identification) cf. *Plectrophenax nivalis* – The proximal part of a right humerus and a complete right wing phalanx were found in the cave in layer D, and a complete left humerus in layer E. The Snow Bunting breeds on bare, rocky lichen tundra of Eurasian Arctic/Alpine zone, but winters in open habitat in the Temperate and Boreal zones (HARRISON 1982). According to TYRBERG (1998) it is known from five Middle and 25 Late Pleistocene localities dispersed in several European countries.

B. Palaeoecological comments

1. Successive layers of sediment

The following brief general characteristics of particular layers including their sedimentology and date (Table IV) are described in details by ŻARSKI (2005). His conclusions on the habitats surrounding the cave in the time periods of accumulation of particular layers do not always correspond with those indicated by the bird assemblages – usually bird remains indicate more often the presence of forests or at least trees.

Layer H is the deepest cave sediment from which bird remains were recorded. These include single bones of two tetraonids, i.e. the Black Grouse and Capercaillie, both found also in the majority of overlaying layers. The latter species was regarded by STEGMAN (1931) as a "taiga species" requiring old mature forest as breeding habitat.

Several clay with rubble layers of series G in the cave provided ten bone fragments of nine individuals representing eight species. All of them were also found in some of the overlaying layers. According to ŻARSKI (2005) the sediments accumulated in the Gniew (= Odderade) Interstadial of the Early Weichselian, in "open and bushy areas". The bird assemblage is too small for good characterization of the environment, but the occurrence of the Crossbill indicates the presence of coniferous trees in which this bird not only nests but also forages.

Layers Gt and Gtx were distinguished in the terrace sediment. Their correlation with series G in the cave is not clear. The former did not contain bird remains, whereas in layer Gtx, from the Late Eemian or Early Glacial according to ŻARSKI (2005), two bird bones were found: the Great Spotted Woodpecker and Blackbird or Song Thrush. These indicate forest or at least parkland habitat with mature deciduous trees (in which the former species excavates nest holes).

The clay with rubble layer F in the cave corresponds with layer Ft in the terrace so we treat them together. ŻARSKI (2005) suggests that this sediment accumulated in the Świecie (= Schaslkholz) Stadial of the Early Glacial. The sediment provided representatives of six bird species only. All were also found in overlaying layers, usually in several ones – with the exception of the House Martin, which besides layer F was found only in layer E.

In part of the terrace sediments, just above layer Ftx, which did not contain bird remains, the layer B/F' was distinguished composed of sandy clay filling gaps among limestone blocks. It seems to be old, however, the dating is not clear but according to ŻARSKI (2005) "it was probably formed during Świecie Stadial". Bird remains found in sediment B/F' consisted of 76 bone fragments of at least 26 individuals, belonging to 13-14 species (besides one fragment identified as the Gyrfalcon

Table IV

Chronostratigraphy, OIS stages, 14C (uncalibrated) and TL dates of particular sediment layers in Komarowa Cave and at the terrace in front, compiled after VAN ANDEL (2003), VAN ANDEL et al. (2003), and ŻARSKI (2005) [Dates in square brackets do not agree with real age of remains]

KA	Chronostratigraphy			OIS stage	Cave layers	Dates BP 14C	Terrace layers	Dates BP 14C and TL*
		Holocene		1	A		A A’	[42200, 46100] [41700]
10	Weichselian (Vistulian)	Late Glacial		2	B		B-B5	9900*, 1150*, 11700*, 12600* 14400*, 16700*
20		Pleniglacial	LGM		C	24450		
30			Denekamp		D	28500, 31100 31400 35500		
40			Hengelo	3	E	39900	Z	37500, 43900
50			Moereshoofd					
60			Świecie (Schalkholz)	4	F		B/F’ Ft, (Ftx?)	[12750*]
70								
80		Early Glacial	Gniew (Odderade)	5a	G		Gtx?	
90				5b	H			
100			Brorup	5c	J, K			
110				5d				
120			E e m	5e				

the other two were determined ambiguously as Gyrfalcon/Saker Falcon). All identified species but the Scaup, the only species recorded exclusively from this layer, were found also in layer B and some also in other layers (Table II). Water-and-marsh species prevail, however the share of land birds is the highest because of the large number of Willow Grouse.

The clay layer E contained limestone rubble therefore, according to ŻARSKI (2005), it accumulated in a cool climate, and the site was surrounded by open habitats "with bushes and single trees". A single radiocarbon date, 39900 BP, indicates an origin in the Interpleniglacial (the date points, according to KOZARSKI 1991, to the Hengelo Interstadial). The bird fauna represents a mosaic of habitats, and does not fully support the above mentioned picture of the habitat as concerns "single trees". Though only two taiga species, i.e. the Capercaillie and Fieldfare, were identified - at least the former needs mature old stands for breeding. Five taxa were exclusively recorded in this layer. Two of these (the Smew and a middle sized duck) belong to anseriforms, but the Smew breeds in tree holes in Boreal forests near fresh waters; the nests of the Spotted Eagles are also situated on trees in mature forests (HARRISON 1982). For the remaining species, generally treated as "forest" ones, lesser forests or thickets may be enough.

Layer D of the cave sediment containing clay and single limestone rubble is a few thousand years younger than layer E, but still from the Interpleniglacial (OIS 3). It provided the richest bird fauna of all layers, consisting of 567 bone remains belonging to at least 107 individuals, and representing 61 taxa (Table I). Four radiocarbon dates (28500 BP, 31100 BP, 31400 BP, and 35500 BP) indicate that this layer accumulated during the Denekamp Interstadial and the end of the previous stadial (KOZARSKI 1991). According to ŻARSKI (2005) the pollen analyses indicate that open habitats with herbaceous plants predominated in the surroundings, but a few species of deciduous trees like alder, birch, hazel, or lime were also present. The latter is supported by finding such bird species as the Fieldfare, Pied Flycatcher, and Golden Oriole breeding in mature deciduous trees. The latter two species also belong to the group of 18 taxa identified exclusively in layer D (in spite of their recent breeding in southern Poland). A few typical Arctic birds such as *Lagopus*, the Golden and Grey Plovers were found together with the southern European Alpine Swift, Alpine Chough, Rock Thrush, or the steppe dwelling Little Bustard, and with various water-and-marsh species.

Layer C deposited only in the cave consisted of clays with limestone rubble. Most of its surface was covered by Holocene layer A. One radiocarbon date, 24550±220 BP, indicated that it accumulated in the early part of the Upper Pleniglacial. It provided 33 bird remains representing at least 13 individuals of 12 taxa. Their composition is however somewhat out of the ordinary, because besides the Snowy Owl and the Grey Plover typical of the Arctic tundra, the Capercaillie typical of taiga mature forest and the Alpine Swift representing the Mediterranean fauna were recorded. The presence of the Capercaillie, Black Grouse, and two thrush species suggests that besides "vegetation characteristic of open and shrubby areas" (ŻARSKI 2005) some parts of the surroundings also had to be forested.

The sandy layer B accumulated in the front part of the cave and at the terrace, with one exception from the terrace sediments (Table II) – in the cave sediment only one fragment of unidentified passerine was found. Four levels were distinguished in part of layer B (B1-B4), but they did not provide bird bones. The deepest part of layer B, denoted B5, contains however a few bone fragments, all belonging to three species also present in the main sediment of layer B, so they are treated together. Bird remains consist of 326 bone fragments representing at least 74 individuals, belonging to 43 taxa. Nine species were recorded in this layer exclusively: six of them are typical for various water-and-marsh habitats, and only three nest in forests and trees or shrubs in open habitats. Generally, 16 species typical for forests were recorded, but only two, i.e. the Capercaillie and Fieldfare, represent the taiga species. The juveniles of three species of grouse, the Yellowhammer and Jackdaw (Table III) indicate breeding near the cave. ŻARSKI (2005) attributes layer B to a cold period between 16700 and 9900 BP, i.e. the end of the Upper Pleniglacial and entire Late Glacial, however, the Late Glacial besides cold periods contains the Bölling and Alleröd interstadials which were much warmer.

Three thin clay flows (Z1 - Z3) are found within the sediment of layer B at the terrace, being the result of solifluction processes and according to ŻARSKI (2005) corresponding to the Interplenigla-

cial sediments (radiocarbon dates: 43900 BP and 37500 BP). These clay layers contained remains of seven bird species. Two species, i.e. the Spotted Redshank and Common Sandpiper, were identified only in the flows. Both are typical of water-and-marsh habitats – the former breeding in the Subarctic and Boreal swamps in open forest or shrub tundra and the latter in all of Europe (HARRISON 1982). Of the remaining five species four were also recorded in at least five other layers of various age, and only an ambiguously identified bone of the Jack Snipe was also found in layer B. So it is impossible to determine if the bird assemblage of the flows is associated more with the cold period of the sedimentation of layer B or with the warm Interpleniglacial layers E and F, indicated by the radiocarbon dates.

In transitional sediment between layers A and B at the terrace only five fragments belonging to three species were found. The most interesting is that of the Golden Eagle (other two fragments of this species were found in older layers of the cave).

The uppermost Holocene layer A accumulated mainly on the terrace in front of the cave. It contained 290 bone fragments, belonging to at least 76 individuals (Table II). This layer was very thin inside the cave providing three bones only (Table I). A distinct layer A' below layer A, in which 15 bones were found, could be resolved in part of the terrace sediment. These fragments represent six taxa identified in main layer A, but also include the Pygmy Owl, so, here we treat them together. Altogether in layer A, 47 taxa of wild birds and the Domestic Hen were identified. Two bones of the Willow Grouse, one of the Capercaillie, and three of a thrush belonged to juveniles (Table III) indicating directly that these species nested in the close vicinity of the cave. The taxa recorded in layer A represent mainly "forest" birds, and among them six, i.e. the Capercaillie, Hazel Hen, Pygmy Owl, Black Woodpecker, Fieldfare, and Redwing were considered as "taiga species" by STEGMAN (1931, 1938). Thirteen taxa (the Hazel Hen, Bar-tailed Godwit, Whimbrel or Curlew, Stock Dove, Cuckoo, Pygmy Owl, Black Woodpecker, Short-toed Lark, Leaf Warbler, Spotted Flycatcher, Great Tit, Blue Tit, and Crow) were found in this layer exclusively. However, the lack of some of these in deeper (older) sediments seems to be more or less accidental, because of their occurrence at other Polish sites in sediments older than the Holocene (BOCHEŃSKI 1993).

2. Temperature changes

The following comments are based on Table V presenting thermal indices calculated according to DEMARCQ and MOURER-CHAUVIRÉ (1976) and mean July temperatures cited or interpolated after LORENC (2004). In this table not all layers are represented (for example layer F), because in some of them the numbers of well identified species were too small for calculating thermal indices. Also, not all indices shown in the table are fully comparable. For example the index of layer C, calculated for 12 individuals only, has lesser value (having a larger error probability) than the indices of layers A, B, D, and E, calculated for 70-107 individuals, belonging to 41-60 taxa. Nevertheless, general changes of temperature in time agree with the data of ŻARSKI (2005). The lowest temperature was during the accumulation of layer B/F', and the highest during the accumulation of layer D in the Denekamp Interstadial.

Thermal indices indicate that mean July temperatures between the Hengelo Interstadial (layer E) and Holocene (layer A) fluctuated between 13.5 and ca 16°C. During this time interval the coldest climate was in the time of sedimentation of layer B, but it was still about three degrees warmer than that of layer B/F'. The radiocarbon dates obtained for layer B indicate the accumulation of its upper part during the Late Glacial (see above). However the thermal indices obtained for sediments in the rock shelter in Krucza Skała (situated not far from Komarowa Cave) and concerning the Late Glacial, balanced between 2.17 and 2.79 (BOCHEŃSKI & TOMEK 2004), and only those calculated for the lower layers (2-4) may correspond with layer B in Komarowa Cave – the others point to higher temperatures. Therefore, it is possible that bird bones from layer B accumulated in cold periods bordering the LGM (layer C).

Table V

Thermal indices based on wild bird assemblages recorded in particular layers of sediment of Komarowa Cave and its terrace, calculated according to DEMARCQ and MOURER-CHAUVIRÉ (1976), and mean July temperatures in °C calculated from these indices, cited or interpolated after LORENC (2004)

Layer	Dates (14C and TL)	No of taxa		MNI		Thermal index	Mean July temperature
		Total in layer	Used for calculations	Total in layer	Used for calculations		
A, A'	Holocene	47	38	80	71	2.62	15.5
B-B5	9900-16700	43	35	74	63	2.36	13.5
C	24500	11	11	12	12	2.50	14.5
D	28500-35500	60	45	107	90	2.67	15.5-16.0
E	39900	41	33	71	63	2.61	15.5
B/F'	12750[1]	14	12	27	25	1.82	10.0-10.5

[1] The date obtained using the TL method concerns the sandy fraction in the upper part of the layer; it is not applicable to the real age of animal remains which is supposed to be the Early Pleniglacial.

The lowest temperature during the accumulation of layer B/F' strictly corresponds with that of OIS-4 shown by the curve cited by VAN ANDEL et al. (2003). It depicts general climate changes in the last 100 thousand years based on investigations of the Greenland ice sheet which, according to the author, may influence Europe also. It does not indicate, among others, a high temperature during the Denekamp in spite of two short time but high oscillations about ca 28000 BP. However, VAN ANDEL (2003) suggests that "the nature of events may have varied between different regions" of Europe, and this may account for the discrepancy.

3. Habitat changes

Bird assemblages recorded in particular layers differ among each other not only systematically (which may be more or less accidental), but also in the share of the four groups of birds living in various habitats (forest, water-and-marsh, open, and rocks) defined in Material and Methods. The results are given in Table VI, and in Figs 4 and 5. As in the temperature changes analysis, only the layers containing more than ten taxa were taken into account (layers B/F', E, D, C, B and A) . In the case of the small sample of layer C, the percentage of taxa may not illustrate the real proportions in nature (being much more accidental than in several times more numerous samples – the most spectacular case is that of the rocky habitat dwellers). The differences in the number of taxa (Fig. 4) are much larger than those of individuals (Fig. 5).

Typical forest birds were identified in all layers (even in Dtx or H, where remains were few). This indicates the presence of forests during the entire time of sedimentation. The share of forest bird taxa is the lowest in Early Weichselian layer B/F' (older assemblages are too sporadic for calculation of the share). Forest species increase in abundance in succeeding layers till layer C accumulated during the beginning of the Upper Pleniglacial, and again decrease in layers B-B5 sedimented during the period of maximum ice sheet transgression in the Upper Pleniglacial and in the Late Glacial. During the accumulation of layers B/F' and B-B5, July temperatures were lower than in other periods (Table V), thus forested areas must have been limited and their tree composition was simple. The general share of forest bird individuals is however the highest in all layers compared. Moreover, it is very similar in all layers but Holocene layer A. Both the number of taxa and their share in the sample are the highest in Holocene layer A, which is evidently connected with the development of forests during the last ten thousand years. It may also indicate that the bird of

Table VI

Comparison of the data concerning bird assemblages (numbers of taxa and percentages) discovered in the sediments of particular layers in Komarowa Cave (cave and its terrace treated together). In every assemblage, four general groups of taxa were distinguished, based on their breeding requirements: forest, water-and-marsh, open and rocks

Layer	Dates: 14C, TL	N %	No of taxa	Breeding habitat				MNI	Breeding habitat			
				Forest	Water	Open	Rock		Forest	Water	Open	Rock
A, A'	Holocene	N	47[1]	30	8	7	2	80	63	8	7	2
		%	100	63.8	17.0	14.9	4.3	100	78.7	10.0	8.7	2.5
B-B5	9900-16700	N	43	16	17	8	2	74	44	19	9	2
		%	100	37.2	39.5	18.6	4.7	100	59.4	25.7	12.2	2.7
C	24500	N	11	7	1	1	2	12	7	1	1	3
		%	100	63.6	9.1	9.1	18.2	100	58.3	8.3	8.3	25.0
D	28500-35500	N	60	29	13	13	5	107	67	13	17	10
		%	100	48.3	21.7	21.7	8.3	100	62.6	12.2	15.9	9.3
E	39900	N	41	19	9	8	5	71	43	9	11	8
		%	100	46.3	22.0	19.5	12.2	100	60.5	12.7	15.5	11.3
B/F'	12750[2]	N	14	4	7	3	–	27	16	8	3	–
		%	100	28.6	50.0	21.4		100	59.3	29.6	11.1	

[1] Domestic Hen not taken into account.
[2] The date obtained using the TL method concerns the sandy fraction in the upper part of the layer; it is not applicable to the real age of animal remains which is supposed to be the Early Pleniglacial.

prey (the Eagle Owl, or also other owl species), whose pellets were the source of remains accumulated in the sediments, preferred to hunt forest birds.

The numbers of bird taxa living in water and other humid habitats are the most diversified. Their share in the prey assemblage was the highest in the Early Glacial (layer B/F') coming up to 50%; the number of bird individuals of this ecological group was the highest also. The share of water-and-marsh birds in the assemblage recorded in the layer B-B5 is also very high but not as much as that in B/F'. The smallest share of water-and-marsh birds in the layer C accumulated in an early stage of the Upper Pleniglacial (in terms of the number of taxa and MNI) probably indicating the driest habitat, but its low values may be also connected with the smallest sample of bird bone remains.

The number of species living in open habitats ranges from one in the layer C (which may be connected with the small total number of taxa recorded) to 13 (layer D – the richest), with the Skylark present in both. Generally, the species was recorded in six layers. If we eliminate the layers of the smallest taxa numbers recorded (C, and B/F'), and compare the shares of birds living in open habitats, the numbers of taxa and the MNI are the highest in layer D from the Denekamp Interstadial, and a little lower in layer E of the Hengelo. This may indicate that in spite of fairly high temperatures (see Table V) open habitats were better developed or diversified than in the other sediments.

Seven bird species identified among the remains found in Komarowa Cave lived originally in rocky habitats (now the Swallow and House Martin are mainly synantropic and their nesting on rocks in Poland are extremely rare or unknown). They are the most numerous (in terms of the number of taxa and the MNI) in sediments accumulated in the Denekamp and Hengelo Interstadials. Four species are southern European and they were not found in earlier sediments than those of the Hengelo. Of the four species, the Rock Thrush is now an extremely scarce breeder in the Carpathians, and the remaining three (the Alpine Swift, Snow Finch and Alpine Chough) are accidental visitors (TOMIAŁOJĆ & STAWARCZYK 2003).

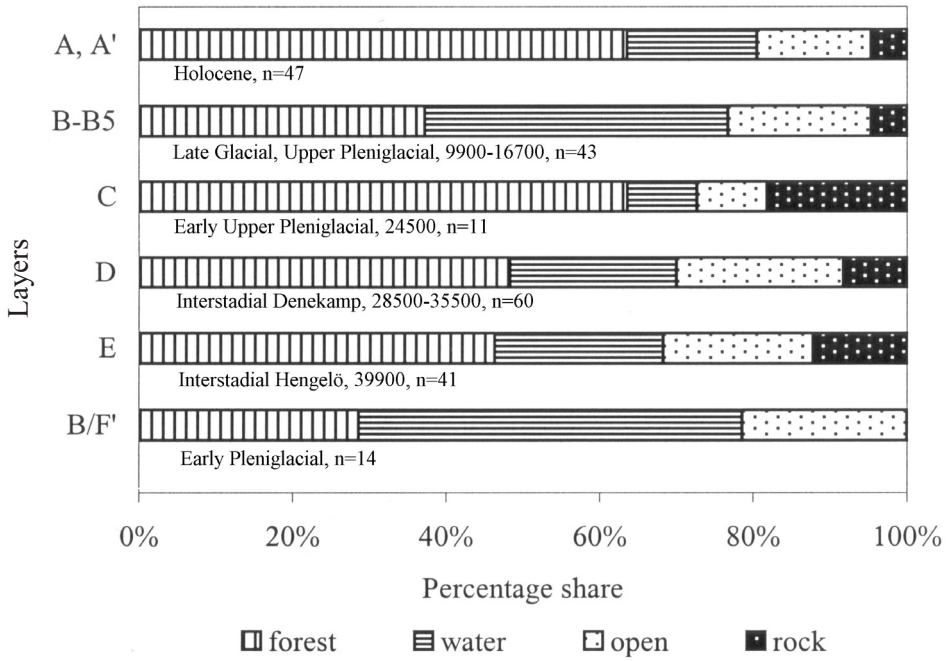

Fig. 4. Percentage share of wild bird taxa (numbers of taxa) breeding in four groups of habitats, excavated in particular sediment layers in Komarowa Cave and terrace in front of it (based on data from Table VI).

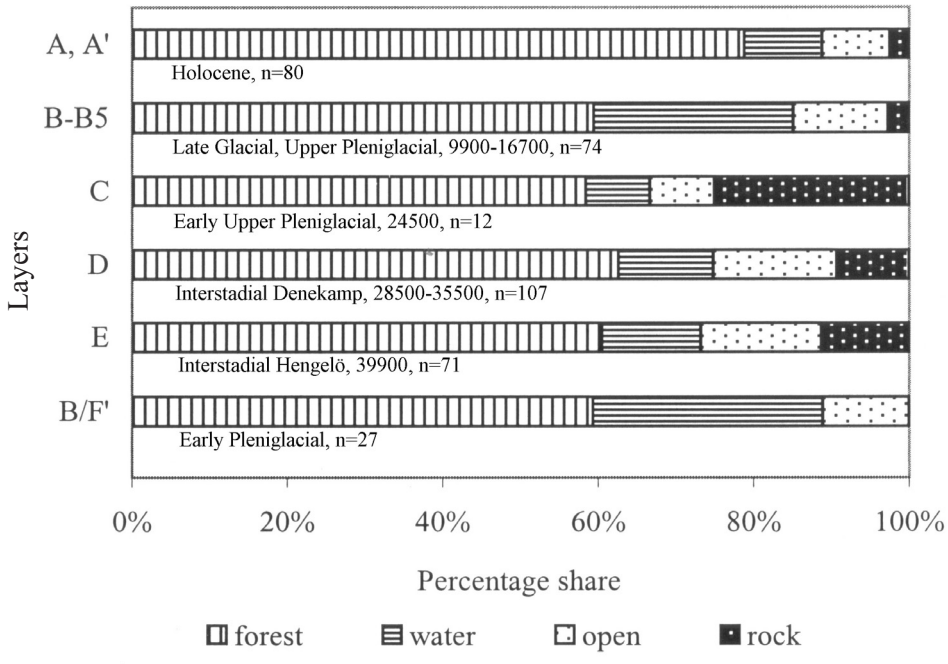

Fig. 5. Percentage share of wild bird taxa (MNI) breeding in four groups of habitats, excavated in particular sediment layers in Komarowa Cave and terrace in front of it (based on data of Table VI).

Generally, proportions among the numbers of taxa and, to a lesser degree, of individuals belonging to forest, water, and open habitat groups indicate the similarity between assemblages found in layers B/F' and B. However, the lack of species breeding in rocks in the former assemblage is very striking; it is not clear if the lack is connected with a small sample, or with other unknown factors. The numbers of taxa and individuals belonging to all four habitat groups are very similar in layers D and E, pointing to similar environmental conditions. The difference between those two layers and layer C (larger share of the rock dwellers) seems to be connected with the difference in the numbers of taxa. The bird assemblage found in layer A is more similar to those of layers C, D, and E than to those of B and B/F', but it differs from the former group in the largest share of the forest birds, especially in their MNI.

C. Zoogeographical comments

The 106 bird taxa identified in Komarowa Cave represent various zoogeographical elements. We do not discuss here the cosmopolitan Peregrine Falcon (VOOUS 1962), numerous Holarctic and European species belonging to the Palaearctic elements. Within the latter category, three groups are of special interest, especially due to their variable share in particular (successive) periods (Tables VII, VIII). The most numerous are "northern" species breeding now in the Arctic and in the case of some of them in the northern part of the Boreal zone. STEGMAN (1938) included 14 species from this group, recorded in Komarowa Cave (Barnacle and Brent Goose, Scaup, Gyrfalcon, Willow Grouse, Ptarmigan, Golden and Grey Plovers, Dotterel, Bar-tailed Godwit, Snowy Owl, Shore Lark, Lapland and Snow Buntings); HARRISON (1982) adds another three (Merlin, Spotted Redshank, and Turnstone). Their recent status in Polish fauna varies. The Scaup exceptionally breeds and regularly migrates in the north, the Golden Plover bred until the 19th cent. and now it regularly migrates, the Dotterel is an extremely rare, sporadic breeder above the timberline of the Tatras and Karkonosze Mts, the Willow Grouse and Ptarmigan, being sedentary, do not visit Poland at all, and all the remaining species belong to regular or irregular migrants or visitors in various numbers, most often in the northern part of the country (TOMIAŁOJĆ & STAWARCZYK 2003). The highest number of species belonging to this group (9 species i.e. 20.9%) was recorded in layer B (B and B5), however their highest share is in the Early Pleniglacial layer B/F' reaching 50,0% (see Table VIII). This may be correlated with very low temperatures.

19 species excavated from sediments of Komarowa Cave were included by STEGMAN (1938) in the "Siberian elements" (Table IX). Most of them are typical forest birds but four represent water-

Table VII

Number of taxa which do not belong to the recent breeding fauna of southern Poland, and recorded in particular layers of Komarowa Cave sediment, and an indication if they breed generally to the north or to the south of this territory

Layer	Dates (14C and TL)	No of taxa	Not reported recent taxa		of them breeding to			
					the north		the south	
			No	%	No	%	No	%
A, A'	Holocene	47	8	17.0	6	12.8	2	4.2
B-B5	9900-16700[1]	43	14	32.6	12	27.9	2	2.7
C	24500	11	4	36.4	3	27.3	1	2.4
D	28500-35500	60	13	21.7	9	15.0	4	6.7
E	39900	41	12	29.3	8	19.5	4	9.8
B/F'	12750[2]	14	7	50.0	7	50.0	–	–

[1] The dates obtained using TL method.
[2] The date obtained using the TL method concerns the sandy fraction in the upper part of the layer; it is not applicable to the real age of animal remains which is supposed to be the Early Pleniglacial.

Table VIII

Share of various faunal elements in wild bird assemblages recorded in particular layers of Komarowa Cave sediments (cave and terrace together), according to STEGMAN (1938). Subarctic = Arctic species living also in the northern part of the Boreal zone

Faunal elements / Particular layers		A,A'	B, B5	Z	C	D	E	F, Ft	B/F'
Total of species		47	43	7	11	60	41	6	14
Arctic, and Subarctic	No	5	9	2	3	8	5	2	7
	%	10.6	20.9	28.6	27.3	13.3	12.2	33.3	50.0
Taiga species (part of Siberian)	No	6	2	1	1	4	3	–	–
	%	12.8	7.0	7.3	9.1	6.7	7.3	–	–
Mediterranean, Mongolian, and Tibetan	No	1	2	–	1	5	4	–	–
	%	2.1	4.7	–	9.1	8.3	9.8	–	–

Table IX

Siberian elements (according to STEGMAN 1938) recorded in particular layers of Komarowa Cave sediments (cave and terrace together). Taiga species are distinguished by the letter "T" after the Latin name. Numbers indicate MNI

Species / Layer		A, A'	B, B5	Z	C	D	E	F, Ft	B/F'	G, Gtx	H
cf. *Mergellus albellus*							1				
Falco tinnunculus						2	1				
Falco subbuteo		1				1	1				
Tetrao urogallus	T	2	1	1	1	1	1				1
Bonasa bonasia	T	1									
Lymnocryptes minimus			3	cf.1							
Tringa erythropus				1							
Tringa cf. *nebularia*			1								
Cuculus canorus		1									
cf. *Strix uralensis*	T					1					
Glaucidium passerinum	T	1									
Dendrocopos major		2								1	
Dryocopus martius	T	2									
Turdus pilaris	T	7	2			2	1				
Turdus cf. *iliacus*	T	1					1				
Phylloscopus cf. *collybita*		2									
Sitta europaea		2				1	1				
Loxia cf. *curvirostra*	T	1				1				1	
cf. *Pyrrhula pyrrhula*	T					1					

and-marsh habitats (Smew, Jack Snipe, Spotted Redshank and Greenshank). Their remains are rare and dispersed. Much more numerous and frequent are remains of forest dwellers. Of these nine are assigned by STEGMAN (1931, 1938) to the "taiga" species (Capercaillie, Hazel Hen, Ural Owl, Pygmy Owl, Black Woodpecker, Fieldfare, Redwing, Common Crossbill, and Bullfinch). All taiga species now belong to the breeding fauna of southern Poland - the Redwing being the rarest and irregular (TOMIAŁOJĆ & STAWARCZYK 2003). The most frequent remains of taiga birds are those of the Capercaillie, recorded since the Early Weichselian layer H until Holocene layer A. The other species, the Fieldfare, is found from Hengelo layer E. The taiga species are most numerously represented in Holocene layer A; only the Ural Owl and Bullfinch are lacking, but both of these birds inhabited again the southern part of Poland in the 20th century. Both were also recorded with three other taiga species in layer D, accumulated in the Denekamp Interstadial. Of the other Siberian forest dwellers, the most frequent are the Hobby and European Nuthatch, both recorded in the Holocene and two Interpleniglacial layers.

Eight bird taxa recorded in Komarowa Cave inhabit now mainly the southern part of Europe. According to STEGMAN (1938) they belong to three faunal elements i.e. the Mediterranean, Mongolian, and Tibetan (Table X). They represent two biotopes i.e. dry open country and rocks. The Crested Lark is the only species breeding now regularly all over the country, the Rock Thrush is an

Table X

"Southern" species, assigned by STEGMAN (1938) to the Mediterranean, Mongolian, and Tibetan faunal elements, recorded in particular layers of Komarowa Cave sediments (cave and terrace together). Numbers indicate MNI

Species \ Layer	A, A'	B, B5	Z	C	D	E	F, Ft	B/F'	G, Gtx	H
Mediterranean:										
Tetrax tetrax					1	1				
Tachymarptis melba				2	2	3				
Mongolian:										
Falco cherrug		1			1					
Calandrella sp.	1									
cf. *Galerida cristata*					2					
cf. *Monticola saxatilis*					1					
Tibetan:										
Montifringilla nivalis	1	1			3	1				
cf. *Pyrrhocorax graculus*						1				

extremely scarce breeder in the Carpathians, but as late as the 20th century it was recorded also in the Kraków-Częstochowa Upland, the Alpine Chough bred in the 19th century in the Tatras and the Little Bustard formerly bred sporadically (TOMIAŁOJĆ & STAWARCZYK 2003). The remaining four species are relatively rare visitors today. All species but one (the Short-toed Lark) were recorded mainly in the Interpleniglacial layers D and E. None of the "southern" species was identified from older sediments (Table X). The remains of the Alpine Swift seem to be the most interesting because of their number (Table I) which indicates the presence of a breeding colony in the Hengelo and Denekamp Interstadials and in the beginning of the Upper Pleniglacial (layer C).

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