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A ZOOARCHAEOLOGICAL AND MOLECULAR ASSESSMENT OF ANCIENT CHICKEN REMAINS FROM RUSSIA¹

© 2021 Ophélie Lebrasseur, Dilyara Shaymuratova, Arthur Askeyev, Gulshat Asylgaraeva, Laurent Frantz, Greger Larson, Oleg Askeyev, Igor Askeyev

We here conduct ancient DNA analyses on 58 chicken bones from 15 archaeological sites (from the 9th to the 18th century AD) across the Volga region, the Leningrad region, the Pskov region, and the north of the Krasnoyarsk region to investigate genetic diversity of past chicken populations within this geographical area. We find all samples belong to sub-haplogroup E1, ubiquitous throughout the world and dominant in Europe, Africa and the Americas. This supports an introduction of chickens from the west, rather than a direct introduction from East Asia. Our study also demonstrates good endogenous DNA content, confirming species identification and sex of the individuals, thus highlighting the potential of genetic studies on archaeological remains in that region.

Keywords: zooarchaeology, Volga region, Russia, Medieval Period, chicken, ancient DNA, dispersal.

Introduction

Chickens play a major role in economies worldwide and provide an efficient source of animal protein to billions of people. Archaeological and palaeogenomics studies have shed light on the mystery surrounding their domestication, but the dispersal of chickens west and introduction to Russia remains relatively unknown.

Chicken domestication

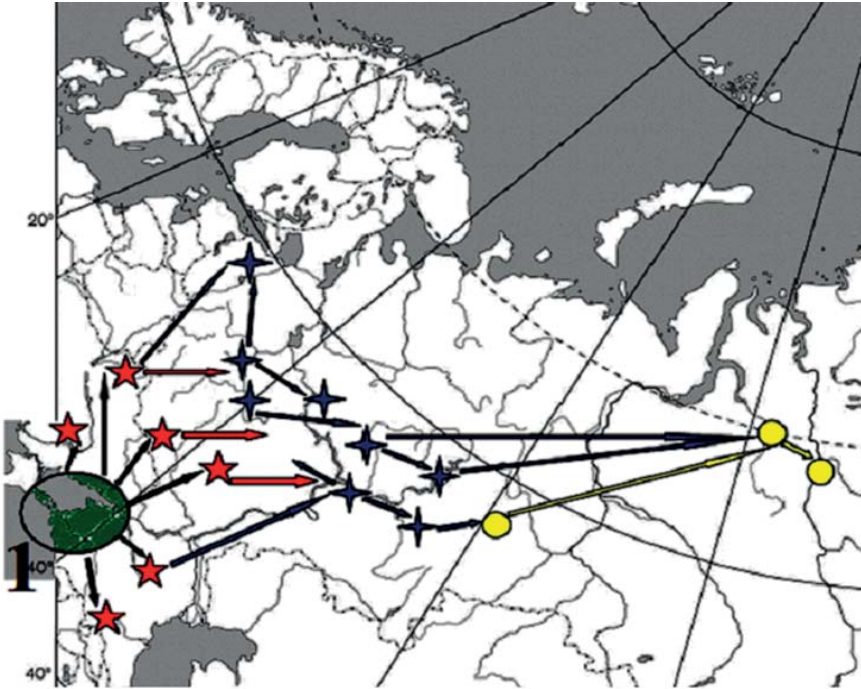
A recent genomic study indicated that chickens were first domesticated in South/Southeast Asia from a Red Jungle fowl subspecies (*Gallus gallus spadiceus*) currently indigenous to Southwestern China, Thailand and Myanmar (Wang et al., 2020). Archaeological evidence suggests chickens were already domesticated by the 2nd millennium BC (Eda et al., 2019; Peters et al., 2016), while molecular data suggest that *G. g. spadiceus* and the domestic lineage diverged around 9500

+/- 3300 years BP (Wang et al., 2020). Altogether, this suggests that chickens were domesticated between ~9500-4000 years ago, although the earliest date is unlikely to reflect the beginning of the domestication process, especially given the lack of archaeological evidence.


Introduction and dispersal of chickens in Russia


Chickens spread across Southeast and South Asia before being introduced further afield. The first evidence of their presence outside of Asia was found on the site of Maresha in Israel dated to the Hellenistic period (4th-2nd century BC) (Perry-Gal et al., 2015). This date also coincides with the appearance of chickens in the Greek colonies of the northern Black Sea region (middle to late 1st millennium BC), where during the existence of the Bosphorus kingdom (5th century BC – 6th century AD), domestic chickens were widespread (Burchak-Abramovich, 1962, p. 438–


¹ OL and GL were supported by Arts and Humanities Research Council (grant number AH/L006979/1). OL, GL and LF were supported by ERC-2013-StG-337574-UNDEAD. GL and LF were supported by Natural Environmental Research Council grants (NE/K005243/1, NE/K003259/1, NE/S007067/1, and NE/S00078X/1). LF was supported by the Wellcome Trust (210119/Z/18/Z). The zooarchaeological research was funded by RFBR, project number 20-09-00004.





1 The initial region of dispersal of domestic chickens into Russia: Northern Black Sea and Azov region in the middle of the 1 millennium BC - the beginning of the 1 millennium AD


 Habitats of domestic chickens at the beginning - the middle of the 1 millennium AD

 The main centers of existence of domestic chickens in Russia in the 9 - 15 centuries AD

 Domestic chickens in Siberia in Russian trading settlements in the 16 - 17 cc. AD

 Directions of the resettlement of domestic chickens at the beginning of the 1 millennium AD

 Directions of the resettlement of domestic chickens in the middle of the 1 millennium AD

 Directions of the resettlement of domestic chickens in Russia in the 9 - 15 centuries AD


 Directions of the resettlement of domestic chickens in Siberia in the 16 - 17 cc. AD

Fig. 1. A map of the distribution of domestic chickens in the territory of European Russia and Siberia according to zooarchaeological studies in the 1st millennium BC – 17th century AD.

Рис. 1. Карта распространения домашних кур на территории Европейской части России и Сибири по данным зооархеологических исследований в I тыс. до н. э. – XVII в. н. э.

440; Burchak-Abramovich, Tsalkin, 1971, p. 54–56, 61).

Later, in the middle of the 1st millennium AD, domestic chickens appear in settlements located at the centre of the European part of Russia and the Volga region (Burchak-Abramovich,

Tsalkin, 1971, p. 54–56, 61; Askeyev et al, 2011, p. 161–163). From the 9th to the 18th century AD, bone remains of domestic chickens become numerous in archaeological sites throughout the European part of Russia (Burchak-Abramovich, Tsalkin, 1969, p. 49–50,

1971, p. 58; Zinoviev, 2009; Askeyev et al, 2011, 2013; Gorobets, Kovalchuk, 2016 p. 5; Shaymuratova et al, 2019, p. 97). This increase in abundance indicates the widespread distribution of domestic chickens amongst past populations, as well as the gradual development of poultry farming and an increasing importance of chickens in the diet (meat and eggs) of historical populations of this region. Finally, the appearance of chickens in Siberia is associated with the establishment of Russian trading settlements on the territory of Western Siberia in the 16th–17th century (Nekrasov, 2003, p. 163–168; Martynovich, 2013, p. 1131) (Figure 1).

Mitochondrial DNA analyses have previously been used to infer domestication and genetic diversity of modern chicken populations worldwide (Liu et al., 2006; Miao et al., 2013). These showed chickens clustered in nine main haplogroups (A-I) and six sub-haplogroups (C1-C3, E1-E3) based on full mitochondrial genomes (Miao et al., 2013), with E1 being ubiquitous throughout the world and dominant in Europe, Africa, and the Americas. Other haplogroups are more geographically restricted: A and B are widely distributed but absent in Africa, C, F and G are found throughout Asia, D is found throughout Asia and Africa but dominates the Pacific, and H and I are restricted to East Asia and South Asia respectively. In addition, wild fowl harboured haplogroups W-Z which are absent in domestic chickens (Miao et al., 2013).

A genetic study conducted on ancient chicken individuals from Germany, Austria, the United Kingdom, and Greece, and spanning the last two millennia, showed E1 was the sole sub-haplogroup found in the past (Girdland-

Flink et al., 2014). More recently, Dyomin and colleagues (2017) sequenced a fragment of the D-loop hypervariable region of the mitochondrial genome of five archaeological chicken bones from the medieval sites of Veliky Novgorod, Pskov, St. Petersburg, Staraya Ladoga, and Azov in the European part of Russia, and dating from the 9th to the 18th century. All but one sample belonged to sub-haplogroup E1, confirming previous findings. The non-E1 haplogroup, C1, was found in a sample from Pskov (18th century) which the authors suggested could have been an exotic import.

Aims and Objectives

The purpose of this paper is to investigate the dispersal of chickens in the Volga region, Russia, based on genetic analyses from samples recovered from 16 archaeological sites spanning the 9th to the 18th centuries AD. More specifically, our aims were the following:

- 1) Assessment of the endogenous DNA content present in the selected bones,
- 2) Confirmation of taxonomic identification and sexing of the individuals,
- 3) Exploration of the genetic diversity of ancient chicken populations in the Volga region.

This is the first genetic study conducted on ancient chicken remains from the vast territory of the Volga region, and will provide valuable information on the dispersal route(s) and settlement process of domestic chickens in this area.

Materials and Methods

Samples

A total of 75 ancient chicken bones spanning the 9th to the 18th centuries AD were obtained from 16 archaeological sites across Russia (Volga region, n=13; Leningrad region, n=1; Pskov, n=1; the north of the Krasnoyarsk region, n=1;

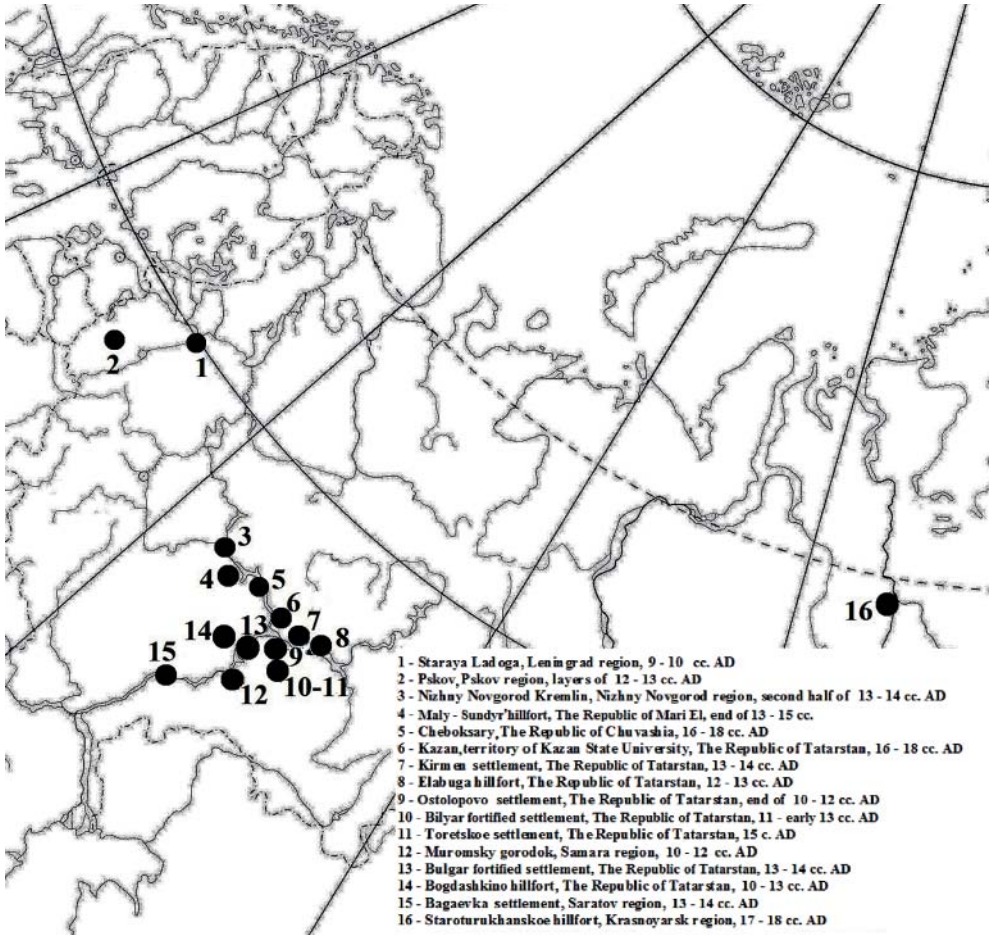


Fig. 2. Map of the archaeological sites with chicken remains.

Рис. 2. Карта с обозначением археологических памятников с остатками домашних кур.

Figure 2, Table 1). The material was recovered during excavations carried out in 2000–2015 mostly from household pits, and, to a lesser extent, from a free cultural layer. All bird remains were hand collected. The identification of bird bones was performed using comparative skeletal collections of birds kept in the Laboratory of Biomonitoring (Institute of Problems in Ecology and Mineral Wealth, Kazan), and following guidelines by Serjeantson (2009).

Coracoids were selected for this study due to their higher bone density (Figure 3). To reduce the likelihood of sampling a same individual twice,

coracoids from one side of the body were used, unless metrics or age proved otherwise.

Ancient DNA extraction

Ancient DNA (aDNA) analyses were undertaken in the dedicated ancient DNA laboratory of the 'Palaeo-BARN', School of Archaeology, University of Oxford (UK). To prevent contamination and ensure the generation of authentic data, strict measures were applied in compliance with standard contamination precautions (Cooper & Poinar, 2000; Gilbert et al., 2005).

Of the 75 samples, we selected 58 for aDNA analyses. Fourteen coracoids

Table 1

List of samples in this study

Sample ID	Chicken Project ID	Site name	Province/Region	Side	Dating/Phasing Information
1	OSO1196	Ostolopovo settlement	The Republic of Tatarstan	Left	end of 9 th – 12 th cc. AD
2	OSO1197	Ostolopovo settlement	The Republic of Tatarstan	Left	end of 10 th – 12 th cc. AD
3*	OSO1198	Ostolopovo settlement	The Republic of Tatarstan	Left	end of 10 th – 12 th cc. AD
4	OSO1199	Ostolopovo settlement	The Republic of Tatarstan	Right	end of 10 th – 12 th cc. AD
5	MUM1200	Muromsky gorodok	Samara region	Left	10 th – 12 th cc. AD
6	MUM1201	Muromsky gorodok	Samara region	Right	10 th – 12 th cc. AD
7	BOG1202	Bogdashkino hillfort	The Republic of Tatarstan	Left	10 th – 12 th cc. AD
8	BOG1203	Bogdashkino hillfort	The Republic of Tatarstan	Left	10 th – 12 th cc. AD
9	BOG1204	Bogdashkino hillfort	The Republic of Tatarstan	Left	10 th – 12 th cc. AD
10**	BIL1205	Bilyar fortified settlement	The Republic of Tatarstan	Right	11 th – early 13 th cc. AD
11**	BIL1206	Bilyar fortified settlement	The Republic of Tatarstan	Right	11 th – early 13 th cc. AD
12	BIL1207	Bilyar fortified settlement	The Republic of Tatarstan	Right	11 th – early 13 th cc. AD
13	BIL1208	Bilyar fortified settlement	The Republic of Tatarstan	Right	11 th – early 13 th cc. AD
14	BIL1209	Bilyar fortified settlement	The Republic of Tatarstan	Right	11 th – early 13 th cc. AD
15**	BIL1210	Bilyar fortified settlement	The Republic of Tatarstan	Right	11 th – early 13 th cc. AD
16*	BIL1211	Bilyar fortified settlement	The Republic of Tatarstan	Left	11 th – early 13 th cc. AD
17	BIL1212	Bilyar fortified settlement	The Republic of Tatarstan	Right	11 th – early 13 th cc. AD
18	BIL1213	Bilyar fortified settlement	The Republic of Tatarstan	Right	11 th – early 13 th cc. AD
19	BIL1214	Bilyar fortified settlement	The Republic of Tatarstan	Right	11 th – early 13 th cc. AD
20**	ELA1215	Elabuga hillfort	The Republic of Tatarstan	Left	layers of 12 th – 13 th cc. AD
21	ELA1216	Elabuga hillfort	The Republic of Tatarstan	Left	layers of 12 th – 13 th cc. AD
22	ELA1217	Elabuga hillfort	The Republic of Tatarstan	Left	layers of 17 th – 18 th cc. AD
23	BUG1218	Bulgar fortified settlement	The Republic of Tatarstan	Right	13 th – 14 th cc. AD
24	BUG1219	Bulgar fortified settlement	The Republic of Tatarstan	Left	13 th – 14 th cc. AD
25	BUG1220	Bulgar fortified settlement	The Republic of Tatarstan	Left	13 th – 14 th cc. AD
26	BUG1221	Bulgar fortified settlement	The Republic of Tatarstan	Left	13 th – 14 th cc. AD
27	TOR1222	Toretskoe settlement	The Republic of Tatarstan	Left	15 th c. AD
28	TOR1223	Toretskoe settlement	The Republic of Tatarstan	Right	15 th c. AD
29	TOR1224	Toretskoe settlement	The Republic of Tatarstan	Right	15 th c. AD
30	TOR1225	Toretskoe settlement	The Republic of Tatarstan	Right	15 th c. AD
31*	TOR1226	Toretskoe settlement	The Republic of Tatarstan	Left	15 th c. AD
32*	TOR1227	Toretskoe settlement	The Republic of Tatarstan	Left	15 th c. AD
33*	TOR1228	Toretskoe settlement	The Republic of Tatarstan	Left	15 th c. AD
34	TOR1229	Toretskoe settlement	The Republic of Tatarstan	Right	15 th c. AD
35	TOR1230	Toretskoe settlement	The Republic of Tatarstan	Right	15 th c. AD
36*	KAZ1231	Kazan, territory of Kazan State University	The Republic of Tatarstan	Left	16 th – 17 th cc. AD
37	KAZ1232	Kazan, territory of Kazan State University	The Republic of Tatarstan	Right	16 th – 17 th cc. AD
38	KAZ1233	Kazan, territory of Kazan State University	The Republic of Tatarstan	Right	16 th – 17 th cc. AD
39	CHB1234	Cheboksary	The Republic of Chuvashia	Right	16 th – 18 th cc. AD
40	CHB1235	Cheboksary	The Republic of Chuvashia	Left	16 th – 18 th cc. AD
41	CHB1236	Cheboksary	The Republic of Chuvashia	Left	16 th – 18 th cc. AD
42	CHB1237	Cheboksary	The Republic of Chuvashia	Left	16 th – 18 th cc. AD
43	CHB1238	Cheboksary	The Republic of Chuvashia	Left	16 th – 18 th cc. AD
44	CHB1239	Cheboksary	The Republic of Chuvashia	Right	16 th – 18 th cc. AD
45*	CHB1240	Cheboksary	The Republic of Chuvashia	Right	16 th – 18 th cc. AD
46	PSK1241	Pskov	Pskov Region	Right	16 th – 18 th cc. AD
47	NNK1242	Nizhny Novgorod Kremlin	Nizhny Novgorod Region	Left	second half of 13 th – 14 th cc. AD
48	NNK1243	Nizhny Novgorod Kremlin	Nizhny Novgorod Region	Left	second half of 13 th – 14 th cc. AD
49	NNK1244	Nizhny Novgorod Kremlin	Nizhny Novgorod Region	Left	second half of 13 th – 14 th cc. AD
50*	NNK1245	Nizhny Novgorod Kremlin	Nizhny Novgorod Region	Right	second half of 13 th – 14 th cc. AD
51*	NNK1246	Nizhny Novgorod Kremlin	Nizhny Novgorod Region	Right	second half of 13 th – 14 th cc. AD
52*	NNK1247	Nizhny Novgorod Kremlin	Nizhny Novgorod Region	Right	second half of 13 th – 14 th cc. AD
53	NNK1248	Nizhny Novgorod Kremlin	Nizhny Novgorod Region	Left	second half of 13 th – 14 th cc. AD
54*	NNK1249	Nizhny Novgorod Kremlin	Nizhny Novgorod Region	Right	second half of 13 th – 14 th cc. AD
55	NNK1250	Nizhny Novgorod Kremlin	Nizhny Novgorod Region	Left	second half of 13 th – 14 th cc. AD
56*	NNK1251	Nizhny Novgorod Kremlin	Nizhny Novgorod Region	Right	second half of 13 th – 14 th cc. AD
57*	NNK1252	Nizhny Novgorod Kremlin	Nizhny Novgorod Region	Right	second half of 13 th – 14 th cc. AD
58	NNK1253	Nizhny Novgorod Kremlin	Nizhny Novgorod Region	Left	second half of 13 th – 14 th cc. AD
59	NNK1254	Nizhny Novgorod Kremlin	Nizhny Novgorod Region	Left	second half of 13 th – 14 th cc. AD
60*	STD1255	Staraya Ladoga	Leningrad region	Left	9 th – 10 th cc. AD
61	STD1256	Staraya Ladoga	Leningrad region	Right	9 th – 10 th cc. AD
62	STD1257	Staraya Ladoga	Leningrad region	Right	9 th – 10 th cc. AD
63*	STD1258	Staraya Ladoga	Leningrad region	Left	9 th – 10 th cc. AD
64	STD1259	Staraya Ladoga	Leningrad region	Right	9 th – 10 th cc. AD
65	STD1260	Staraya Ladoga	Leningrad region	Right	9 th – 10 th cc. AD

66	STD1261	Staraya Ladoga	Leningrad region	Right	9 th – 10 th cc. AD
67	STD1262	Staraya Ladoga	Leningrad region	Right	9 th – 10 th cc. AD
68	STH1263	Staroturukhanskoe hillfort	Krasnoyarsk region	Right	17 th – 18 th cc. AD
69	STH1264	Staroturukhanskoe hillfort	Krasnoyarsk region	Left	17 th – 18 th cc. AD
70*	BAG1265	Bagaevka settlement	Saratov region	Right	13 th – 14 th cc. AD
71*	BAG1266	Bagaevka settlement	Saratov region	Left	13 th – 14 th cc. AD
72	KIR1267	Kirmen settlement	The Republic of Tatarstan	Right	13 th – 14 th cc. AD
73	KIR1268	Kirmen settlement	The Republic of Tatarstan	Right	13 th – 14 th cc. AD
74	MAO1269	Maly Sundryr' hillfort	Republic of Mari El	Right	end of 13 th – 15 th cc. AD
75	MAO1270	Maly Sundryr'hillfort	Republic of Mari El	Right	end of 13 th – 15 th cc. AD

* *Samples excluded for ancient DNA analyses.*

** *Samples for which amplification has failed.*

were thus excluded as neither their side, metrics nor age could confirm individual status (Table 1). A few others were rejected due to their juvenile age (samples 70 and 71). To reduce environmental contamination, 0.5 mm of the bone surface was removed using a Dremel 3000 electric hand-drill. A fragment weighing 150–450 mg was excised from each bone based on good macroscopic preservation. Each sample was grounded to fine powder using a Retsch MM400 microdismembrator. Ancient DNA extractions were performed following the Dabney protocol (Dabney et al., 2013).

Illumina Sequencing Library preparation and capture

Double-strand Illumina libraries were built following Meyer & Kircher (2010), with the addition of a six base-pair barcode added to the IS1_adapter. P5 adapter. The libraries were amplified on an Applied Biosystems StepOnePlus Real-Time PCR system to confirm the library had been successfully built and to determine the optimal number of cycles for the indexing amplification PCR reaction. A six base-pair barcode was added during the indexing amplification reaction resulting in each library being double-barcoded. Following amplification, the samples were run on an Agilent TapeStation 2200 to confirm successful amplification, then pooled equimolarly prior to cleaning with a QIAquick PCR purification

Kit (QIAGEN Ltd, UK) following the manufacturer's instructions.

In addition, we captured a total of 36 amplified libraries using MYcroarray mitochondrial MYbaits with 24 hours hybridisation at 55°C, following the MYbaits manual V3 instructions (2016). All libraries were sequenced on an Illumina HiSeq 2500 (Single End 80bp) sequencer at the Danish National High-Throughput Sequencing Centre, Copenhagen, Denmark.

Initial Quality Control and FastQ Screen

Adapters were removed using AdapterRemoval v2.0.0 (Schubert et al., 2016). Samples were run through FastQ Screen (Wingett & Andrews, 2018) using the BWA algorithm (Li & Durbin, 2009) for species identification based on a database comprising the full mitochondrial genomes of chicken (KX987152), turkey (NC010195), peacock (NC024533), Guinea fowl (KY865420) and goose (MK133021).

Data processing

Reads were aligned using Burrows-Wheeler Aligner (BWA) version 0.7.5ar405 (Li & Durbin, 2009) to Galgal4, with default parameters apart from disabling the seed option ("1 1024") (Schubert et al., 2012). FilterUniqueSAMCons (Kircher, 2012) was then used to remove duplicates. BAM files from different libraries were merged using the MergeSamFiles tool from Picard v1.129 (<http://broadinstitute>).



Fig. 3. Photos of selected coracoids used in this study. Details of each bone can be found in Table 1.

Рис. 3. Фото кораконидов домашних кур, которые были отобраны для данного исследования. Подробное описание каждой кости находится в Таблице 1.

github.io/picard/). We generated mitochondrial genome consensus by obtaining a majority consensus sequence for all samples that had at least 3x average

coverage excluding bases within 5bp of the start and end of a read, and using reads with $BQ \geq 20$ and $MAPQ \geq 30$ as implemented in htsbox: <https://github.com>.

com/lh3/htsbox. Sexing was conducted using a read depth-based method based on Skoglund et al. (2013), comparing alignment of sequencing reads post filtering for a mapping quality q30 to the W chromosome and chromosome 1.

Phylogenetic analysis

Fifty modern chicken mitochondrial genomes representing each haplogroup from Miao et al., (2013) were downloaded from Genbank for haplogroup identification (GU261674-GU261719, HQ857209-HQ857212). Multiple sequence alignments of both these published samples and samples from our study were completed using MAFFT v7.123b, and verified manually through Aliview v1.26 (Larsson, 2014). A phylogenetic tree was produced using IQ tree, where the best fitting-model was identified as TIM2+F+I+G4 (Hoang et al., 2018; Kalyanamoorthy et al., 2017; Minh et al., 2020).

Results

Zooarchaeological assessment of species abundance

We investigated the bird remains from 20 archaeological sites in the Middle Volga region dating from the Medieval to the Post-Medieval period. Starting from the 10th century AD, domestic chickens were dominant amongst remains: out of 6463 bird bones, 3982 bones (61,6%) belonged to domestic chickens (Askeyev et al., 2013, p. 120–123; our unpublished data). In the two archaeological sites of North-West Russia – in the layers of medieval Staraya Ladoga (9th–10th cc. AD) and Pskov (12th–13th cc. AD) – a substantial number of domestic chicken bones have also been found. However, for Staraya Ladoga, wild bird remains still predominate over domestic birds, with a ratio of 1079 bones of wild birds (80,8%) to 225 bones of domestic chickens (16,8%) (Shaymaratova et al,

2019, p. 96–97). In the Pskov strata, the remains of domestic chickens prevail in number over the remains of wild birds: this was noted both for the early urban layers (12th–13th cc. AD) and for later layers (end of 13th – early 18th cc. AD) (Shaymuratova, Askeyev, 2017, p. 64, tab. 1). Thus, according to the zooarchaeological material we have analysed for the territory of the Volga region and North-West Russia, by the 13th century, domestic chickens were becoming one of the main domestic animals. Regarding the Staroturukhanskoe hillfort (17th – 18th cc. AD) geographically located on the territory of Western Siberia, 29 bones of domestic chickens belonging to adults were identified, placing them as the fourth most abundant bird remains after wild species. Such a relatively small number of bones of domestic birds is typical for northern Post-Medieval settlements (Nekrasov, 2003; Martynovich, 2013), which is associated with the difficult climatic conditions and limited opportunities for raising and keeping domestic animals. However, the discovery of bones from adult individuals of domestic chickens indicates their existence and importance in the diet and economic life of the population of that time.

We have previously published in detail the results of a zooarchaeological study of chicken remains from the Volga region, their numbers on individual archaeological sites, size, age and sex composition of the flock, as well as their relationship with other identified bird species (see Askeyev et al., 2011, 2013; Galimova et al., 2014). This is thus not considered in detail in this article.

Species Identification

Of the 58 samples selected for genetic analyses, 54 were successfully

Table 2

Genetic Results

Sample ID	Site	Genetics ID	Species ID (Genetics)	Screening Results		Mitochondrial Capture Results				
				Total Reads	% Mapped Reads Once Duplicates Removed	Haplogroup	Sex Calls	Depth	Coverage	% Mapped Reads Once Duplicates Removed
1	Ostolopovskoe settlement	OL1676	<i>Gallus gallus</i>	827472	0,79	E1	N/A	27,2	1,0	14,04
2	Ostolopovskoe settlement	OL1677	<i>Gallus gallus</i>	1107822	59,14	E1	Female	24,3	1,0	79,32
4	Ostolopovskoe settlement	OL1679	<i>Gallus gallus</i>	1202591	5,04	E1	Female	12,5	1,0	15,95
5	Muromsky gorodok	OL1572	Not enough reads	7111	0,62	-	-	-	-	-
6	Muromsky gorodok	OL1576	<i>Gallus gallus</i>	1365216	44,60	E1	Female	59,5	1,0	77,51
7	Bogdashkinskoe hillfort	OL1655	<i>Gallus gallus</i>	692574	3,62	E1	Male	40,3	1,0	50,19
8	Bogdashkinskoe hillfort	OL1656	<i>Gallus gallus</i>	325533	2,00	E1	Male	19,8	1,0	38,21
9	Bogdashkinskoe hillfort	OL1675	<i>Gallus gallus</i>	617277	3,75	E1	Female	9,7	1,0	35,06
12	Bilyar hillfort	OL1680	<i>Gallus gallus</i>	796628	3,29	E1	Female	10,7	1,0	33,25
13	Bilyar hillfort	OL1673	<i>Gallus gallus</i>	572301	10,64	E1	Female	16,9	1,0	47,31
14	Bilyar hillfort	OL1672	Not enough reads	891	0,22	-	-	-	-	-
17	Bilyar hillfort	OL1594	<i>Gallus gallus</i>	1117975	3,16	E1	Female	38,9	1,0	33,61
18	Bilyar hillfort	OL1595	<i>Gallus gallus</i>	648762	7,56	E1	Female	38,3	1,0	58,05
19	Bilyar hillfort	OL1596	<i>Gallus gallus</i> *	675564	0,37	-	-	-	-	-
21	Elabuga hillfort	OL1598	<i>Gallus gallus</i>	2343501	1,03	E1	Female	10,9	1,0	11,29
22	Elabuga hillfort	OL1599	<i>Gallus gallus</i>	455829	5,05	E1	Male	11,7	1,0	38,88
23	Bulgar	OL1593	<i>Gallus gallus</i> *	487747	0,48	E1	N/A	3,5	1,0	10,51
24	Bulgar	OL1587	<i>Gallus gallus</i>	1206097	0,86	E1	Male	4,5	1,0	12,31
25	Bulgar	OL1591	<i>Gallus gallus</i>	460718	11,59	E1	Female	25,2	1,0	65,55
26	Bulgar	OL1590	<i>Gallus gallus</i>	1508172	11,09	E1	Female	70,5	1,0	59,39
27	Toretskoe settlement	OL1581	<i>Gallus gallus</i>	891445	2,32	E1	Male	23,6	1,0	34,30
28	Toretskoe settlement	OL1578	<i>Gallus gallus</i> *	148175	2,81	-	-	-	-	-
29	Toretskoe settlement	OL1583	<i>Gallus gallus</i>	1458885	1,84	E1	Female	4,5	1,0	6,55
30	Toretskoe settlement	OL1582	Not enough reads	19199	1,68	-	-	-	-	-
34	Toretskoe settlement	OL1577	<i>Gallus gallus</i> *	24933	26,04	E1	Female	1,3	0,7	48,80
35	Toretskoe settlement	OL1654	<i>Gallus gallus</i>	2522615	0,72	E1	Female	12,6	1,0	14,97
37	Kazan city, territory of Kazan State University	OL1584	<i>Gallus gallus</i>	2591876	4,96	E1	Female	59,0	1,0	43,78
38	Kazan city, territory of Kazan State University	OL1659	<i>Gallus gallus</i>	1578223	0,83	E1	Male	8,7	1,0	10,47
39	Cheboksary city	OL1588	<i>Gallus gallus</i>	1860607	38,39	E1	Female	71,7	1,0	71,01
40	Cheboksary city	OL1585	<i>Gallus gallus</i>	1175959	16,46	E1	Female	22,0	1,0	49,19
41	Cheboksary city	OL1589	<i>Gallus gallus</i> *	71971	5,28	E1	Female	0,4	0,3	23,52
42	Cheboksary city	OL1586	<i>Gallus gallus</i> *	670751	0,20	E1	N/A	0,2	0,1	4,34
43	Cheboksary city	OL1651	<i>Gallus gallus</i> *	818368	0,97	-	-	-	-	-
44	Cheboksary city	OL1592	<i>Gallus gallus</i> *	394859	1,40	E1	Male	3,6	0,9	16,47
46	Pskov city	OL1662	-	283728	0,64	-	-	-	-	-

47	Nizhny Novgorod Kremlin	OL1665	<i>Gallus gallus</i> *	57583	3,92	-	-	-	-	-
48	Nizhny Novgorod Kremlin	OL1573	<i>Gallus gallus</i> *	244507	2,00	-	-	-	-	-
49	Nizhny Novgorod Kremlin	OL1658	<i>Gallus gallus</i> *	1599846	0,24	E1	Female	1,6	0,7	1,63
53	Nizhny Novgorod Kremlin	OL1574	<i>Gallus gallus</i>	432125	13,98	E1	Female	12,6	1,0	55,30
55	Nizhny Novgorod Kremlin	OL1575	Not enough reads	46067	1,39	-	-	-	-	-
58	Nizhny Novgorod Kremlin	OL1666	<i>Gallus gallus</i>	639438	11,52	E1	Male	36,6	1,0	58,22
59	Nizhny Novgorod Kremlin	OL1579	<i>Gallus gallus</i>	612521	13,82	E1	Female	7,1	1,0	38,21
61	Staraya Ladoga	OL1670	<i>Gallus gallus</i>	3078340	1,23	E1	Female	6,8	1,0	3,86
62	Staraya Ladoga	OL1678	<i>Gallus gallus</i> *	49068	2,16	-	-	-	-	-
64	Staraya Ladoga	OL1669	<i>Gallus gallus</i> *	389184	0,60	E1	Female	1,3	0,7	10,47
65	Staraya Ladoga	OL1657	<i>Gallus gallus</i> *	1191888	0,11	-	-	-	-	-
66	Staraya Ladoga	OL1663	<i>Gallus gallus</i>	888972	0,67	-	-	-	-	-
67	Staraya Ladoga	OL1664	<i>Gallus gallus</i> *	705244	0,16	-	-	-	-	-
68	Staroturukhanskoe hillfort	OL1667	<i>Gallus gallus</i> *	70906	1,09	-	-	-	-	-
69	Staroturukhanskoe hillfort	OL1661	<i>Gallus gallus</i> *	77652	2,72	E1	Female	2,6	0,9	36,34
72	Kirmenskoe settlement	OL1580	<i>Gallus gallus</i> *	257085	0,27	-	-	-	-	-
73	Kirmenskoe settlement	OL1660	<i>Gallus gallus</i> *	786797	0,61	-	-	-	-	-
74	Malo-Sundryrskoe hillfort	OL1653	<i>Gallus gallus</i>	1265238	2,16	E1	Male	27,2	1,0	31,95
75	Malo-Sundryrskoe hillfort	OL1650	Not enough reads	2659774	0,01	-	-	-	-	-

* <50 reads

amplified and screened for an initial assessment of DNA content and quality (Table 2, Figure 4). All samples with sufficient mitochondrial DNA sequences were identified as *Gallus gallus* through FastQ Screen, confirming morphological identification (Table 2).

Full mitochondrial genomes

For each sample, the total number of reads, and percentage of reads aligned to the chicken genome after duplicate removal are listed in Table 2. The latter ranged up to 59% with no distinct pattern based on the samples' age (Figure 4). It is worth noting though that samples from Staraya Ladoga (samples 61–67), Staroturukhanskoe hillfort (samples 68, 69), Kirmen settlement (samples 72, 73) and Maly Sundryr' hillfort (74, 75) yielded very little DNA.

Based on these results, 36 samples were then selected for mitochondrial

capture (BioProject Accession number PRJEB40810), for which the depth, coverage and percentage of reads aligned to the chicken genome are listed in Table 2. Thirty-four samples had good coverage; the percentage of sequenced reads mapping to the genome once duplicates were removed ranged from 10% to 79% with four samples below 10% (samples 29, 42, 49 and 61). Coverage depth ranged from 1.3x to 71.7x, with the exception of samples 41 and 42 which had both low coverage (<0.5) and low depth (<1x).

For phylogenetic analysis, the full mitochondrial genome sequences generated were first aligned to 50 sequences previously published by Miao et al. (2013) and representing the 19 mtDNA haplogroups and sub-haplogroups the authors identified. We also included the current chicken

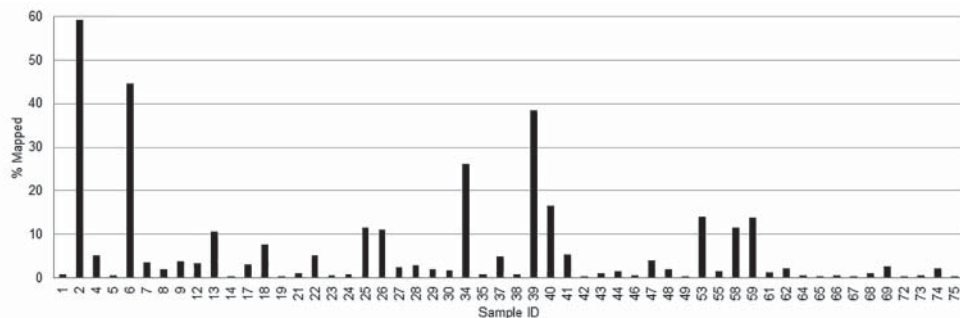


Fig. 4. Screening results – Percentage of reads aligned to the chicken genome once duplicates removed.

Рис. 4. Результаты скрининга – процент считываний, совпадающих с геномом домашней курицы после удаления дубликатов.

full mitochondrial genome reference NC_040970. The haplogroup nomenclature follows Miao et al. (2013). The results clearly show all samples fall within the E1 sub-haplogroup (Figure 5).

Sexing Identification

With the exception of three samples which did not possess enough reads to confidently infer the sex (samples 1, 23, 42), we found a large majority of the individuals (72.7%) were females. The sites containing more than one individual, the Ostolopovo settlement, Bilyar fortified settlement and Staraya Ladoga consisted solely of female samples.

Discussion

Fifty-eight samples from 15 sites and spanning the last millennium were assessed for DNA content, with 36 of these (62%) containing good endogenous DNA content for mitochondrial DNA capture. No correlation between DNA preservation and age of the samples was observed. This suggests good endogenous DNA preservation in archaeological bird remains, at least over the last 1200 years, and demonstrates the potential of aDNA analyses on ancient bones from birds and other animals from this region.

Species identification was positively confirmed for half of the individuals (53%). Nineteen samples contained <50 mitochondrial reads which nevertheless aligned to *Gallus gallus*, suggesting that these samples were indeed chickens. The remaining five samples did not yield enough reads for conclusive species identification. The quality of endogenous DNA permitted sex identification, demonstrating the value of aDNA analyses in providing additional information on the individual and consequently the population when no diagnostic features can be identified morphologically.

Interestingly, all samples sequenced in this study belonged to the E1 sub-haplogroup, ubiquitous throughout the world and dominant in the West. In fact, E1 was previously shown to be fixed in ancient European chickens (Dyomin et al., 2017; Girdland Flink et al., 2014). This finding suggests that chickens from the Volga region were introduced from Western Europe rather than Asia. This fits well with the zooarchaeological data suggesting that chickens were first introduced in the mid-first millennium BC through the Greek colonies in the Northern Black Sea region, after which,

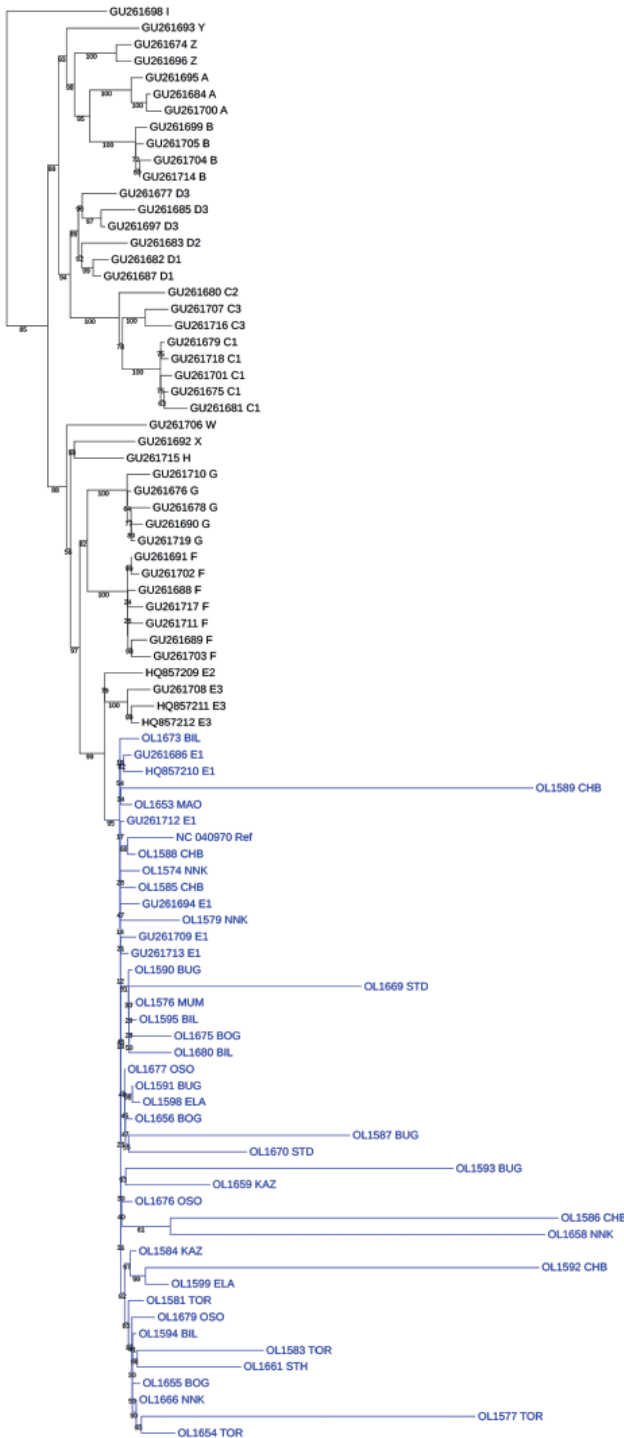


Fig. 5. Maximum-likelihood tree based on full mitochondrial genomes from 50 published samples (denoted by their GenBank Accession number) and samples from this study (OLXXXX). Haplogroups are indicated by the letter following the GenBank Accession number in the published samples. The E1 sub-haplogroup is coloured in blue. BIL = Bilyar fortified settlement, BOG = Bogdashkino hillfort, BUG = Bulgar fortified settlement, CHB = Cheboksary, ELA = Elabuga hillfort, KAZ = Kazan, MAO = Maly Sundyr' hillfort, MUM = Muromsky gorodok, NNK = Nizhny Novgorod Kremlin, OSO = Ostolopovo settlement, STD = Staraya Ladoga, STH = Staroturukhanskoe hillfort, TOR = Toretskoe settlement.

Рис. 5. Дерево максимального правдоподобия, созданное на основе полных митохондриальных геномов из 50 опубликованных образцов (обозначены их регистрационные номера в ГенБанке) и образцы из данного исследования (OLXXXX). Г-апогруппы обозначаются буквой после регистрационного номера ГенБанка в опубликованных образцах. Под-г-апогруппа E1 окрашена в синий цвет. BIL = Биллярское городище, BOG = Богдашкинское городище, BUG = Булгар, CHB = Чебоксары, ELA = Елабуга, KAZ = Казань, MAO = Мало-Сундырское городище, MUM = Муромский городок, NNK = Нижний Новгород (Кремль), OSO = Остолоповское селище, STD = Старая Ладога, STH = Старотуруханское городище, TOR = Торецкое поселение.

beginning of the first millennium AD and with the development of trade between the Bosphorus kingdom and neighbouring regions, they expanded throughout the Northern Black Sea region, the Don region, the Dnieper region, the North Caucasus, and the centre of the European part of Russia and Volga region.

Chicken remains, however, are rare during these periods and their distribution across settlements is uneven. They only become ubiquitous by the end of the 9th century to the beginning of the 12th century AD, in almost all settlements in the centre of the European part of Russia and in the Middle Volga. This increase in chicken consumption is likely the result of migration and expansion of the Slavic population into the central and north-western parts of the Russian Plain, and of the Bulgar population into the Volga region from the lands of the Khazar Kaganate (Don and Kuban region), and which began during the 9th century AD. During the 12th and 15th centuries AD, chickens headed east and northeast to the Vyatka Territory, the Urals, the Middle Urals and the Sursky region with the Slavic-Russian (Novgorod and Vladimir-Suzdal) colonisation movement. Chickens were also widespread within large state formations including the Golden Horde and the Kazan Khanate. By the end of the 14th – 15th centuries AD, domestic chickens were present and abundant throughout the European part of Russia. The active development of the Russian territory of Western Siberia at the end of the 16th century – 17th century AD, which accompanied the development of trading settlements, led to the introduction of chickens in Siberia.

The lack of non-E1 (sub)-haplogroups amongst our assemblages does not

confirm nor refute the hypothesis of a secondary introduction of chickens by Slavic and Bulgar populations around the 11th century as chickens become more abundant in archaeological layers. However, it does support an introduction from the Black Sea region or Europe into the Volga region as a direct introduction from the East would most likely have resulted in the presence of non-E1 haplogroups as suggested by Dyomin and colleagues (Dyomin et al., 2017). Indeed, the latter identified an 18th century sample from Pskov belonging to the C1 sub-haplogroup, and suggested it may have been brought from Western Europe into Russia as Pskov was part of the Hanseatic league. Alternatively, the sample could have been introduced into Europe from China via Russia given the close economic ties between the last two.

Conclusion

Our research has shown a successful combination of zooarchaeological and genetic tools for studying the bones of domestic chickens. Through the large amount of chicken remains found on archaeological sites and the research methodology applied, we have reconstructed more than a thousand-year history of the evolution of the domestic chicken in Russia with special attention to the Volga region. We have established that all our samples belong to sub-haplogroup E1, which is ubiquitous throughout the world. This sheds some light on the monogenic origin of ancient chickens from the study area. The good preservation of endogenous DNA demonstrates the potential of ancient genetic research on bird bones from medieval and post-medieval archaeological sites in this region.

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ЗООАРХЕОЛОГИЧЕСКАЯ И МОЛЕКУЛЯРНАЯ ОЦЕНКА ДРЕВНИХ ОСТАТКОВ ДОМАШНИХ КУР ИЗ РОССИИ

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В данной статье представлены результаты исследований авторами древней ДНК, извлеченной из 58 костей домашних кур, костные остатки которых происходили из 15 археологических памятников средневековья (IX–XVIII вв. н.э.) 4-х регионов России - Поволжья, Ленинградской области, Псковской области и севера Красноярского края, чтобы исследовать генетическое разнообразие прошлых популяций кур в этой географической области. Нами выявлено, что все протестированные образцы костных остатков кур принадлежат к субгаплогруппе E1, распространенной во всем мире и доминирующей в Европе, Африке и Америке. Этот вывод подтверждает факт прихода домашних кур в Европейскую часть России с Запада, а не прямую интродукцию из Восточной Азии. Наше исследование также демонстрирует хорошее содержание эндогенной ДНК, подтверждающее идентификацию вида и пола, тем самым подчеркивая потенциал генетических исследований костных остатков животных из археологических памятников исследуемой территории.

Ключевые слова: зооархеология, Поволжье, Россия, средневековье, домашняя курица, древняя ДНК, расселение.

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