DOI: 10.17746/1563-0110.2016.44.3.139-149

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Dental Anthropology of the Mesolithic and Neolithic Populations of the Eastern European Forest-Steppe Zone*

Dental data are used to test two hypotheses as to whether the "eastern" traits of the Mesolithic and Neolithic populations of the Russian Plain are due to Mongoloid admixture or to evolutionary conservatism: specifically, to the retention of features peculiar to the Upper Paleolithic groups. Frequencies of nonmetric traits (both those used in standard population studies and so-called markers of generalized conservatism) were studied in dental samples from Yuzhny Oleniy Ostrov and Vasilyevka-3 (Mesolithic), Fomino (Ryazan variant of Pit-Comb Ware culture), Karavaikha (Kargopol variant of the same culture), Vovnigi-1 (Kiev-Cherkassy variant of the Neolithic Dnieper-Donets culture), and Vovnigi-2 (Azov-Dnieper variant of the same culture). Published dental data on Zvejnieki (Mesolithic Kunda culture), Yasinovatka and Nikolskoye (Dnieper-Donets culture), Sakhtysh-2a (Lyalovo variant of the Neolithic Pit-Comb Ware culture), and Upper Paleolithic samples from Europe were used for comparison. Both A.A. Zubov's standard protocol and C.G. Turner's ASUDAS were employed. The results suggest that multiple evolutionary processes were involved. Northeastern European Mesolithic dentitions indicate both Mongoloid admixture and continuity with Upper Paleolithic groups. Mesolithic series from Ukraine are more specialized in the Caucasoid direction, while also showing certain Upper Paleolithic traits. In the Neolithic, the dental differences between northern and southern Caucasoids decrease, and there is a gradual reduction of both Mongoloid and Upper Paleolithic characteristics. Nonetheless, people of the Pit-Comb Ware culture, like those of Dnieper-Donets culture display certain Upper Paleolithic traits, which are the most evident in Vovnigi-2.

Keywords: *Upper Paleolithic, Mesolithic, Neolithic, dental anthropology, evolutionary conservatism.*

Introduction

The population history of the Mesolithic and Neolithic groups of the Russian Plain is one of the most hotly debated topics in Russian physical anthropology. There are two main views on the topic. The first view explains the cranial morphology of the Mesolithic and Neolithic population as a result of an admixture between European Caucasoid and East Asian or Siberian (Mongoloid) groups (Benevolenskaya, 1984; Denisova, 1997; Zhirov, 1940). The second view considers the craniological type of the population as "evolutionarily conservative" or "undifferentiated" and retaining ancient Upper Paleolithic morphology (Gokhman, 1986: 219; Yakimov, 1958: 90). The first view has been prevalent in the anthropological literature for a long time. But at the moment, the most popular paradigm considers both Caucasoids and Mongoloids as descendants of "boreal Eurasians", and thus the cranial morphology of the Neolithic population is interpreted as "undifferentiated" with respect to modern races' morphology, or "evolutionarily conservative" (Chikisheva, 2012: 179).

*Supported by the Russian Science Foundation (Project No. 14-50-00036).

However, there are some trends in recent scientific literature reviving this long-standing debate about the population history of the forest belt of the Russian Plain. Firstly, there is a growing tendency in the literature to use the terms "undifferentiated" and "evolutionarily conservative" as synonyms, despite substantial differences between the two. The first term can be used in the broad sense and applied to any group that morphologically does not fit well in the modern racial classification. By contrast, "evolutionary conservatism" necessarily means retention of a complex of traits typical of the group ancestral to both descendant populations: those populations relative to which a group can be called "evolutionarily conservative". The importance of correct use of both terms is particularly evident when discussing the Mesolithic and Neolithic population of the Russian Plain. In this case, the morphology of a skeletal sample can be considered "undifferentiated" even if it emerged as a result of an ancient admixture between populations that were not descended from a recent common ancestor. Such a situation can occur, for instance, if there were "Protomongoloids" among the ancestors of a group, as the morphology of "Protomongoloids" differs substantially from that of modern Mongoloid populations. But to call an ancient population "evolutionarily conservative", a researcher should convincingly demonstrate the persistence of some morphological traits typical of the Mesolithic and Neolithic groups—descendants of the Upper Paleolithic Europeans.

Secondly, according to the results of recent population genetic studies, subclades of the mtDNA haplogroup C were widely dispersed throughout the Russian Plain during Mesolithic and Neolithic times. Those haplogroups are found in at least three archaeological samples: the Mesolithic Yuzhny Oleniy Ostrov at Lake Onega (Der Sarkissian et al., 2013), and the Neolithic Nikolskoye and Yasinovatka sites (Newton, 2011: Tab. 4) in the Dnieper River region. The haplogroup C is considered a typical Eastern Eurasian haplogroup, found with highest frequencies in Central and Southern Siberian populations (Balanovskaya, Balanovsky, 2007: 142). As it has never (so far) been found in the Upper Paleolithic specimens from Eastern Europe, a migration from the East becomes a plausible explanation of its appearance in the Mesolithic and Neolithic groups.

Methods

In this study, the two following hypotheses were examined: that there was a gene-flow from Eastern Eurasian Mongoloid groups to the Mesolithic and Neolithic population of the forest belt of the Russian Plain; and that there was an "evolutionarily conservative" component in the gene pool of this population, arising from the Upper Paleolithic population. In order to test the hypotheses we aimed, firstly, to trace the chronological dynamics of the frequencies of the dental traits marking Mongoloid dental complex; and, secondly, to assess to what extent the studied samples are similar to the Upper Paleolithic population of Europe. The Mongoloid dental complex traditionally includes the following traits: shoveling of the upper central incisors, the distal trigonid crest, and six-cusped lower first molars. These traits are a part of the conventional set of traits used in Russian dental anthropology for inter-population comparisons. The set also includes frequencies of four-cusped lower first and second molars, deflecting wrinkles on the lower first molars, hypocone reduction on the maxillary second molars, and odontoglyphic variant 2med(II) (the distal groove of metaconid falls into the fissure separating the metaconid and the protoconid) (Zubov, 1968, 2006).

Another set of traits was designed specifically for assessing the degree of "evolutionary conservatism" of the dental complex of a sample and its probable similarity to Upper Paleolithic morphology (Zubova, 2013). The set includes phenes that are typical of the Upper Paleolithic samples but rare in modern populations. The pattern of variation of these phenes in modern Eurasians is "mosaic", and thus one of them taken alone does not have a great taxonomic value. But in the Upper Paleolithic, these traits assemble in different localities to form unique dental complexes, and those complexes could be of great importance when studying inter-population continuity.

In our study, the set of traits marking "evolutionary conservatism" includes: labial convexity, lingual fovea, finger-like projections, and the lingual inclination of the upper incisors crowns; distal and mesial accessory ridges of upper and lower canines; rhomboid crown shape, crista oblique, metaconulus, and the odontoglyphic variant 1Pr(II) (the distal protocone groove falls into the fissure separating the protocone and paracone); anterior and posterior fovea of the upper and lower molars; shoveling of the lower incisors; accessory cusps of the lower premolars; derivatives of cingulum on the premolars and molars; and middle trigonid crest of lower molars. Grade scales for all traits in Russian dental system and ASUDAS are shown in Table 1.

Material*

Our dental sample included the following collections representing the Mesolithic and Neolithic sites of the

*The author expresses her gratitude to the skeletal collection curators at the Peter the Great Museum of Anthropology and Ethnography (MAE) RAS (St. Petersburg) and Anuchin Research Institute and Museum of Anthropology of MSU (Moscow) for access to material.

Table 1. **Dental traits used in this study, and their grade scales**

Trait	Key teeth	A.A. Zubov's dental system	Archaic features accounting	ASUDAS	Source (trait and scale description)
			Maxilla		
Shoveling	I^1	2–3	–	2–7	(Zubov, 1968, 2006; Turner, Nichol, Scott, 1991)
Labial convexity	I^1	–	2–4	2–4	(Turner, Nichol, Scott, 1991)
Lingual fovea	I^1	–	+	–	(Zubova, 2013)
Finger-like projections	I^1, C	+	1–3	+	(Zubov, 1968; Zubova, 2013)
Lingual inclination of the crown	I^1	–	+	–	(Zubova, 2013)
Hypocone reduction	M^2	3, 3+	–	0–3	(Zubov, 1968; Turner, Nichol, Scott, 1991)
Carabelli cusp	M^1	2–5	–	2–7	(Zubov, 1968, 2006; Turner, Nichol, Scott, 1991)
Rhomboid crown shape	M^1	–	+	–	(Bailey, 2004)
Crista oblique	M^1	+	3	+	(Zubov, 1968; Zubova, 2013)
Metaconulus	M^1	+	+	–	(Zubov, Khaldeyeva, 1993)
1Pr(II)	M^1	+	+	–	(Zubov, 1974)
Anterior fovea	M^1	+	+	+	(Scott, Turner, 1997)
Posterior fovea	M^1	+	+	+	(Ibid.)
			Mandible		
Mesial accessory ridge	C	+	2–3	2–3	(Zubov, Khaldeeva, 1993; Turner, Nichol, Scott, 1991)
Distal accessory ridge	C	1–5	1–5	1–5	(Scott, 1977)
Crown asymmetry	P_1, P_2	+	+	+	(Bailey, 2002)
Additional mesial lingual cusps	P_1, P_2	–	+	–	–
Additional distal lingual cusps	P_1, P_2	–	+	–	–
Cingulum	M_1	–	+	–	(Zubov, 1960)
Hypoconulid	M_1	$5M_1 + 6M_1$	–	1–5	(Zubov, 1968; Turner, Nichol, Scott, 1991)
Four-cusped M_2	M_2	+	–	+	(Ibid.)
Six-cusped M_1	M_1	+	–	+	"
Distal trigonid crest	M_1	+	–	+	"
Middle trigonid crest	M_1	+	+	+	(Zubov, 1992)
Deflecting wrinkle	M_1	+	–	2–3	(Zubov, 1968; Turner, Nichol, Scott, 1991)
Anterior fovea	M_1	+	+	+	(Turner, Nichol, Scott, 1991)
Posterior fovea	M_1	+	+	+	–
Central cusp	M_1	–	+	–	(Khaldeyeva, Kharlamova, Zubov, 2010)
2med(II)	M_1	+	–	–	(Zubov, 2006)
2med(III)	M_1	+	–	–	(Ibid.)
1med/1prd	M_1	1, 2, 3	–	–	"

Russian Plain: Mesolithic from Yuzhny Oleniy Ostrov in Karelia (Onega culture, 7th–6th millennia BC, MAE RAN collection No. 5773) and Vasilyevka-3 in the Dnieper River region (MAE RAN collection No. 6462); Neolithic from Chernaya Gora (Fomino) burial grounds, Ryazan variant of the Pit-Comb Ware culture (4th–3rd millennia BC (Arkheologiya…, 1996: 378) (MSU collection No. 89: No. 2–6, 10, 13, 14, 16–18); Karavaikha, Kargopol variant of the same culture (4th–mid 3rd millennia BC (Ibid.) (MSU collection No. 8622–8625, 8761, 9788); and Vovnigi-1 (Kiev-Cherkassy variant of the Neolithic Dnieper-Donets culture), and Vovnigi-2 (Azov-Dnieper variant of the same culture) (MAE collection No. 6204; MSU collection unnumb.). All these samples were studied using both the conventional set of dental traits and the "evolutionary conservatism" set of traits (Table 2).

Additional reference data were a Mesolithic sample from Zvejnieki (Mesolithic Kunda culture, Latvia), two Neolithic samples of Dnieper-Donets culture from Dnieper Nadporozhye region (Yasinovatka, Nikolskoye), and a sample from Sakhtysh-2a (Lyalovo variant of the Neolithic Pit-Comb Ware culture). These samples were studied using only the conventional set of traits (Table 2), and were used mostly to examine the possible Mongoloid admixture in the Neolithic population of Eastern Europe.

Frequencies of dental traits in a combined sample of the Upper Paleolithic specimens from Kostenki XIV, XV, XVIII and Sungir 2, 3 (Table 3) were used as a "reference" dental complex in respect of which the chronological dynamics of the traits frequencies have been assessed. A description of the Kostenki XVIII dentition was published by N.I. Khaldeyeva (2006), Sungir, by A.A. Zubov (2000), and the specimens from Kostenki XIV (MAE, No. 6463-1) and XV (MAE, No. 6109-1) were examined by the author. Finally, published data on the Early and Late Upper Paleolithic European population (Manni, Vargiu, Coppa, 2007) were also used in this study (Table 3).

Results and discussion

Upper Paleolithic data. As mentioned in our previous publications, the specimens from the forests-steppe zone of the Russian Plain all represent the same dental complex. Typical of this complex are the absence of marked shoveling of the upper medial central; elevated occurrence of Carabelli cusp and distal accessory cusps of the upper first molars; considerable reduction of hypocone on the upper second molars; and the absence of six-cusped lower molars, *tami*, and distal trigonid crest in the lower first molars. Other distinctive features are a predominance of Y-pattern on the lower first molars and a rather high occurrence of four-cusped lower second molars (Zubova, Chikisheva, 2015: 143). This combination of traits is generally similar between our and other researchers' data (Table 3); but it is of note that, owing to differences between research protocols, our data are not fully comparable with those of the Western and Central European studies. The main difference between the Russian (Sungir and Kostenki) and European specimens is the absence of the six-cusped lower first molars, of distal accessory ridges on upper and lower canines, of shoveling of the lower incisors, and of epicristid in lower molars in the Russian specimens (Table 3).

According to existing data, there are two different dental variants in the Paleolithic population of the forest-steppe zone of the Russian Plain: one is represented at the Sungir site, and another in the Kostenki-Borshchevo archaeological records. The Sungir variant is characterized by a greater robustness of the dentition, and also the presence of deflecting wrinkles on the lower first molars (Ibid.); while the Kostenki complex is characterized by a marked gracility of the dentition. A set of "evolutionarily conservative" traits shared by most Upper Paleolithic fossils includes labial convexity of the vestibular surface of medial incisors; lingual inclination of their crowns; and complete posterior foveae or their elements on upper first molars. The Kostenki XVIII individual also showed posterior foveae on lower molars. In the Kostenki XIV fossil, a peculiar morphology of lower premolars, different from both Neanderthal and modern dentition, was observed. The Sungir specimens exhibit a hypertrophy of hypocone, finger-like projections of upper incisors and canines, a complex ("Neanderthaloid") shape of lower premolar, cingulum of lower molars and central cusp, and type 3 of the first eocone (paracone) groove, often considered a marker of the Eastern dental meta-race (Zubov, 2006: 50). Notably, the distribution of other odontoglyphic phenes, typically used for distinguishing between populations of the Eastern and Western dental meta-races, is different in the Upper Paleolithic specimens as compared to modern population. The relationship between the confluence points of the first metacone and eocone (protocone) grooves on the upper first molars is represented by variants 2 and 3; type 1, most common in Caucasoids, is absent here (Ibid.: 56). The same situation is observed for the distribution of variants of the confluence of the second metaconid fissure on lower first molars. In both cases, when its direction could be reliably traced (Sungir 2 and Kostenki XV), it fell into the intertubercular fissure III, thus showing the absence of 2med(II) phene, typical of Caucasoid populations. The first grooves of metaconid and protoconid in these specimens join fissure II together, forming a neutral combination from the point of view of racial differentiation.

Table 2. **Dental trait frequencies in the Mesolithic and Neolithic samples**

Trait	Yuzhny Oleniy Ostrov		Zvejnieki*		Fomino		Karavaikha		Sakhtysh-2a		Vasilyevka-3		Vovnigi-1		Vovnigi-2		Yasinovatka**		Nikolskoye**	
	n (*N*)	%	*n* (*N*)	%	*n* (*N*)	%	*n* (*N*)	%	*n* (*N*)	%	*n* (*N*)	%	*n* (*N*)	%	*n* (*N*)	%	*n* (*N*)	%	*n* (*N*)	%
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Maxilla																				
Shoveling	...	12*	...	26.7	0 (7)	0	0 (3)	0	0 (7)	0	0 (5)	0	0 (2)	0	1 (14)	7.14	0 (12)	0	0 (2)	0
Labial convexity	1 (7)	14.3	...	...	0 (4)	0	1 (3)	33.3	...	...	0 (5)	0	0 (2)	0	0 (21)	0	...	...	...	...
Lingual fovea	0 (9)	0	...	...	0 (4)	0	0 (3)	0	...	...	0 (5)	0	0 (1)	0	0 (20)	0	...	...	...	...
Lingual inclination of the crown	0 (5)	0	...	...	0 (4)	0	0 (3)	0	...	...	0 (5)	0	0 (2)	0	0 (21)	0	...	...	...	...
Finger-like projections I1	2 (7)	28.6	...	...	1 (4)	25	0 (3)	0	...	...	1 (5)	20	0 (1)	0	3 (19)	15.79	...	...	...	...
Finger-like projections C	0 (9)	0	...	...	1 (4)	25	0 (4)	0	...	...	0 (5)	0	0 (1)	0	3 (21)	14.3	...	...	...	...
Distal accessory ridge	0 (9)	0	...	...	0 (4)	0	0 (4)	0	...	...	2 (5)	40	0 (2)	0	4 (21)	19.05	...	...	...	...
Mesial accessory ridge	0 (9)	0	...	...	0 (4)	0	0 (4)	0	...	...	0 (5)	0	0 (2)	0	0 (21)	0	...	...	...	...
Rhomboid crown shape	1 (24)	4.2	...	...	0 (8)	0	0 (4)	0	...	...	0 (8)	0	0 (11)	0	3 (42)	7.1	...	...	...	...
Carabelli cusp	...	30.8*	...	64.7	6 (8)	75	1 (4)	25	4 (12)	33.3	1 (7)	14.3	2 (8)	25	8 (21)	38.1	8 (23)	34.8	3 (15)	20
Crista oblique	0 (9)	0	...	...	2 (6)	33.3	1 (4)	25	...	...	0 (4)	0	0 (5)	0	2 (16)	12.5	...	...	...	...
Metaconulus	0 (2)	0	...	...	1 (6)	16.7	0 (4)	0	...	...	0 (2)	0	0 (6)	0	0 (12)	0	...	...	...	...
Anterior fovea	0 (6)	0	...	...	0 (6)	0	0 (4)	0	...	...	0 (2)	0	0 (3)	0	0 (20)	0	...	...	...	...
Posterior fovea	0 (7)	0	...	...	0 (6)	0	0 (3)	0	...	...	0 (5)	0	0 (4)	0	1 (22)	4.54	...	...	...	...
1Pr(II)	...	...	...	...	2 (3)	66.7	…	...	...	...	...	...	0 (3)	0	0 (3)	0	...	...	...	...
Hypocone reduction	...	26.2*	...	18.2	3 (11)	27.3	4 (5)	80	3 (8)	37.5	6 (9)	66.7	3 (13)	23	15 (27)	55.56	2 (19)	10.5	2 (14)	14.3

Table 2 (end)

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Mandible																				
Shoveling	0 (13)	0	...	...	0 (3)	0	0 (3)	0	...	...	0 (7)	0	0 (3)	0	0 (22)	0	...	...	...	...
Distal accessory ridge	0 (12)	0	...	...	0 (5)	0	0 (4)	0	...	...	1 (10)	10	0 (6)	0	0 (23)	0	...	...	...	...
Mesial accessory ridge	0 (12)	0	...	...	0 (5)	0	0 (4)	0	...	...	0 (10)	0	0 (6)	0	0 (23)	0	...	...	...	...
Mesial accessory cusps P1	0 (20)	0	...	...	0 (4)	0	0 (4)	0	...	...	0 (8)	0	0 (8)	0	1 (26)	3.84	...	...	...	...
Distal accessory cusps P1	0 (20)	0	...	...	0 (4)	0	0 (4)	0	...	...	0 (8)	0	0 (8)	0	0 (26)	0	...	...	...	...
Cingulum M1	0 (29)	0	...	...	0 (8)	0	0 (4)	0	...	...	0 (12)	0	0 (12)	0	0 (35)	0	...	...	...	...
Six-cusped M1	...	12.5*	...	11.5	1 (7)	14.3	0 (4)	0	3 (13)	27	1 (12)	8.33	0 (9)	0	0 (23)	0	2 (22)	9.1	1 (11)	9.1
Four-cusped M1	...	3.5*	...	0	0 (7)	0	0 (4)	0	0 (13)	0	0 (12)	0	0 (12)	0	0 (24)	0	0 (22)	0	0 (11)	0
Distal trigonid crest	...	10.9*	...	0	2 (8)	25	0 (4)	0	2 (11)	18.18	0 (6)	0	0 (9)	0	0 (16)	0	0 (14)	0	0 (10)	0
Epicristid	0 (19)	0	...	...	0 (7)	0	0 (3)	0	0 (11)	0	0 (6)	0	0 (9)	0	0 (35)	0	...	...	...	...
Deflecting wrinkle	...	15.4*	...	10.6	1 (5)	20	0 (4)	0	1 (5)	20	0 (2)	0	0 (4)	0	0 (6)	0	0 (6)	0	0 (6)	0
Anterior fovea	0 (8)	0	...	...	0 (6)	0	0 (2)	0	...	...	0 (5)	0	0 (5)	0	0 (21)	0	...	...	...	...
Posterior fovea	0 (14)	0	...	...	0 (6)	0	0 (3)	0	...	...	0 (5)	0	0 (5)	0	0 (25)	0	...	...	...	...
Central cusp	0 (7)	0	...	...	0 (7)	0	0 (3)	0	...	...	0 (6)	0	0 (8)	0	1 (28)	3.57	...	...	...	...
1med/1prd1	0 (1)	0	...	...	0 (1)	0	0 (2)	0	...	...	2 (2)	100	0 (1)	0	0 (3)	0	...	...	...	...
1med/1prd2	1 (1)	100	...	...	1 (1)	100	2 (2)	100	...	...	0 (2)	0	0 (1)	0	3 (3)	100	...	...	...	...
1med/1prd3	0 (1)	0	...	...	0 (1)	0	0 (2)	0	...	...	0 (2)	0	1 (1)	100	0 (3)	0	...	...	...	...
2med(II)	1 (4)	25	...	...	2 (5)	40	1 (2)	50	...	...	1 (2)	50	...	...	1 (6)	16.7	0 (7)	0	1 (6)	16.7
2med(III)	2 (4)	50	...	...	3 (5)	60	0 (2)	0	...	...	1 (2)	50	...	...	0 (6)	0	6 (7)	85.7	3 (6)	50
Four-cusped M2	...	55.5*	...	80.8	5 (8)	62.5	4 (4)	100	...	...	8 (11)	72.72	8 (9)	88.88	19 (24)	79.17	20 (23)	86.9	12 (15)	80

* Data after (Denisova, Graudonis, Gravere, 1985).

** Data after (Segeda, 2013).

Table 3. **Dental trait frequencies in the Upper Paleolithic European specimens**

Trait	Kostenki and Sungir		Early Upper Paleolithic Europe		Late Upper Paleolithic Europe	
	n (*N*)	%	*n* (*N*)	%	*n* (*N*)	%
Maxilla						
Shoveling	0 (4)	0	1 (20)	5	0 (19)	0
Labial convexity	2 (4)	50	10 (23)	43.5	8 (19)	42.1
Lingual fovea	0 (3)	0	...	...	...	...
Lingual inclination of the crown	2 (4)	50	...	...	...	...
Finger-like projections I1	1 (3)	33.3	…	31.2	6 (16)	37.5
Finger-like projections C	1 (3)	33.3	9 (10)	90	14 (24)	58.3
Distal accessory ridge	0 (3)	0	2 (5)	40	10 (20)	50
Mesial accessory ridge	0 (3)	0	0 (7)	0	0 (22)	0
Rhomboid crown shape	1 (5)	20	...	...	...	...
Carabelli cusp	2 (5)	40	9 (21)	42.9	21 (37)	56.8
Crista oblique	0 (4)	0	...	...	...	...
Metaconulus	0 (4)	0	...	...	...	...
Anterior fovea	0 (4)	0	...	...	...	...
Posterior fovea	2 (4)	50	...	...	...	...
1Pr(II)	0 (2)	0	...	...	...	...
Hypocone reduction	2 (4)	50	…	40	15 (45)	33.3
Mandible						
Shoveling	0 (3)	0	…	9.1	0 (31)	0
Distal accessory ridge	0 (3)	0	8 (15)	53.3	8 (26)	30.8
Mesial accessory ridge	0 (3)	0	...	...	...	...
Mesial accessory cusps P1	0 (2)	0	...	...	...	...
Distal accessory cusps P1	0 (2)	0	...	...	...	...
Cingulum M1	1 (4)	25	...	...	...	...
Six-cusped M1	0 (5)	0	…	6.1	3 (44)	6.8
Four-cusped M1	1 (5)	20	...	...	...	...
Distal trigonid crest	0 (4)	0	...	...	...	...
Epicristid	0 (4)	0	4 (17)	23.5	7 (22)	31.8
Deflecting wrinkle	1 (4)	25	1 (2)	50	2 (13)	15.4
Anterior fovea	0 (4)	0	...	...	6 (12)	50
Posterior fovea	1 (5)	20	...	...	...	...
Central cusp	1 (3)	33.3	...	...	...	...
1med/1prd1	1 (2)	50	...	...	...	...
1med/1prd2	0 (2)	0	...	...	...	...
1med/1prd3	1 (2)	50	...	...	...	...
2med(II)	0 (2)	0	...	...	...	...
2med(III)	2 (2)	100	...	...	...	...
Four-cusped M2	4 (4)	100	30 (37)	81.1	40 (49)	81.6

Mesolithic data. The Mesolithic samples from Yuzhny Oleniy Ostrov and Vasilyevka-3 differ substantially. The former retains the elevated occurrence of Carabelli cusp, deflecting wrinkle, and a prevalence of the five-cusped lower first molars: a combination typical of the Upper Paleolithic groups. The distribution of odontoglyphic phenes can be described only in very general terms, because of strong dental attrition. Phene 2med(II) is present in the sample, but occurs more rarely as compared to 2med(III). The relationship between confluence points of the first metaconid and protoconid grooves with the intertubercular fissure is only represented by variant 1, as in the Paleolithic. At the same time, the full trait complex marking the Eastern dental meta-race is present in the sample, though most traits are found with low frequencies: marked shoveling of upper incisors, sixth cusp on lower first molars, prevalence of the five-cusped lower second molars, and the distal trigonid crest (see Table 2). Nevertheless, the maxillary complex of the sample retains many of the "evolutionarily conservative" traits commonly found in the Upper Paleolithic skulls: labial convexity of medial incisors, posterior fovea of the upper molars, and finger-like projections of the upper incisors and canines. There was also a case of the rhomboid upper molar in the sample, similar to the Sungir 2 specimen.

But the Vasilyevka-3 sample displays a morphology which is much closer to that of typical Caucasoid groups. The two most important "Mongoloid" traits—the upper incisors' shoveling and the distal trigonid crest—are absent in the sample; the six-cusped lower molars are less frequent, while the four-cusped lower second molars are more frequent. The "evolutionary conservatism" traits are much less common in this sample. From the whole set of "conservative" traits, there were observed only finger-like projections in the upper incisors and canines (Table 2). 2med (II) and 2med(III) variants were found just one time each.

The Mesolithic Zvejnieki sample is intermediate between the two above-mentioned samples in terms of the prevalence of the traits of the conventional set. The Eastern dental meta-race markers in the sample are represented by the upper incisors' shoveling and six-cusped lower molars, while the distal trigonid crest is absent (Table 2).

Neolithic data. In the sample from Fomino (Ryazan variant of the Pit-Comb Ware culture), the following markers of the Eastern dental meta-race were observed: the six-cusped lower first molars, distal trigonid crest, and increased frequency of the five-cusped lower second molars; while the medial incisor shoveling was absent (Table 2). There were several cases of weakly pronounced marginal ridges of the lingual surface of the incisors, but they never reached grade 2 of the standard scale. Gracile types of the lower first molars are absent in the sample, while the deflecting wrinkle of metaconid and the elevated occurrence of the Carabelli cusp are present. Such a combination is also observed in the Mesolithic population of the Baltic region. The "evolutionary conservatism" markers are virtually absent in Ryazan sample (just one case of the mesostylid in the lower second molar). Turning to the odontoglyphic phenes, there were two cases of the distal groove of protocone merging with the fissure II, variant 2 of the relationship between confluence points of 1med and 1prd, and an increased frequency of the "Eastern" variant 2med(III) as compared to 2med(II).

At Karavaikha (Kargopol variant of the Pit-Comb Ware culture), there were no "Eastern" markers found in the sample, while the "evolutionary conservatism" set was represented only by labial convexity of upper incisors (see Table 2); the Carabelli trait frequency is increased, the deflecting wrinkle is absent. Odontoglyphic phene 2med (II) is present, 2med(III) is absent. The relationship between confluence points of the first metaconid and protoconid grooves could be recorded in only one case, when 1med merged with the intertubercular fissure lower than 1prd. The Sakhtysh-2a sample (Lyalovo variant of the same culture) is similar to the Karavaikha in terms of the prevalence of traits of the conventional set: the upper medial incisors' shoveling is also absent, but the frequency of the six-cusped lower first molars is increased; whereas the frequency of the four-cusped second molars is decreased. The distal trigonid crest and deflecting wrinkle of the metaconid are also present.

In the Neolithic samples from the Ukraine, the markers of the Eastern dental meta-race are virtually absent, despite their earlier dates as compared to the Northern Neolithic samples. The samples of the Dnieper-Donets culture (Yasinovatka, Nikolskoye, Vovnigi-1) are very similar to the Mesolithic sample from Vasilyevka-3. The dental complex, common to all these groups, includes absence of the upper incisors' shoveling, four-cusped lower first molars, distal trigonid crest, and the deflecting wrinkle; a moderate frequency of the Carabelli cusp, and low reduction level of the maxillary molars (Table 2). Of the "Eastern" markers, there are only six-cusped lower molars found in the sample with a very moderate frequency, which in fact fits to the modern Caucasoid range of this trait (Table 2). In the only sample examined for the "evolutionary conservatism" markers (Vovnigi-1), they were not found in the key teeth at all.

The Vovnigi-2 samples display a slightly different dental complex as compared to other Ukrainian groups. First of all, a case of marked shoveling of the upper incisors was observed; but more importantly, the morphology of the dentition was much more "evolutionarily conservative". In this sample were observed the finger-like projections

of upper incisors and canines, the distal accessory ridge of upper canines, posterior fovea on upper first molars, and several cases of the hypocone hypertrophy. In the lower premolars, a mesial accessory cusp was found, and in the lower molars, a central accessory cusp. Such a dental complex makes the Vovnigi-2 sample similar to the Upper Paleolithic groups of Europe.

Our results led us to conclusion that both main views on the formation of distinctive dental morphology of the Mesolithic and Neolithic population in the Russian Plain were valid and well-based. But the history of this population as reconstructed from the dental non-metrics variation is slightly different from the results of craniometric studies.

Our results for the Mesolithic Yuzhny Oleniy Ostrov sample (Onega culture) help to resolve the contradiction between the two opposite points of view: E.V. Zhirov's (1940), G.F. Debets' (1956), Y.D. Benevolenskaya's (1984), and R.Y. Denisova (1997) on the one hand, and V.P. Yakimov's (1958) on the other hand. One can see a persistence of the "evolutionarily conservative" dental complex, similar to the Upper Paleolithic morphology. Most of the "evolutionary conservatism" markers, found in the ancient European specimens, are present in the sample. But at the same time, as was suggested by the previous studies, the presence of the Eastern dental meta-race markers shows that another dental complex, brought in by ancient Mongoloid migrants, was also present in the sample (Zubova, 2012). The dental complex of the Vasilyevka-3 sample is more specialized. Both "evolutionarily conservative" and Mongoloid complexes are reduced, and the frequencies of most phenes fit into the range of variation of the modern Central European dental type.

The trends of dental variation found in the Mesolithic age continue in the Neolithic samples. Neolithic populations can be divided into two groups, according to their cultural and chronological attribution. The first group includes the population of the forest belt (Pit-Comb Ware culture), while the second includes representatives of the Dnieper-Donets culture.

In most Northern groups, some markers of the Eastern dental meta-race are still found, but correlations between single traits are disturbed. Thus, shoveling of upper incisors has not been observed in any of the Neolithic samples, while the distal trigonid crest and the six-cusped lower first molars are found. This suggests, not that the Mongoloid dental complex *per se* was included in the Pit-Comb Ware population; but rather, that the presence of the Eastern phenes may be explained by admixture with the Mesolithic groups of mixed ancestry. This probable admixture most likely affected different populations to different extents. For instance, Benevolenskaya wrote about the similarity of two out of three Neolithic skulls from Karavaikha to the "euryprosopic (low-faced) type of Oleniy Ostrov", which was, in her opinion, of Eastern origin (1984: 50). But unlike Yuzhny Oleniy Ostrov, in the Karavaikha sample the Mongoloid markers are absent, as well as the markers of "evolutionary conservatism" (excluding labial convexity of the upper incisors). Though the latter trait is single and not a part of a dental complex, its presence may link the sample to the more ancient "evolutionarily conservative" groups. The Ryazan dental complex is different: the markers of the Eastern dental meta-race are prevalent (excluding shoveling of the upper incisors), while labial convexity of incisors is absent. The "evolutionary conservatism" set is only represented by the finger-like projections of upper frontal teeth, crista oblique, and metaconulus on upper molars. Thus, both dental complexes simultaneously present in the Mesolithic population of the North of the Russian Plain ("evolutionarily conservative" and Mongoloid) in the Neolithic groups were probably eliminated partially by genetic drift.

By contrast, dental morphology in the samples of the Dnieper-Donets representatives did not change substantially in comparison with the Mesolithic population. The Eastern markers are absent in most samples. The six-cusped lower molars are the only ubiquitous trait; but owing to its low frequency, this does not have a serious taxonomic value. The "evolutionary conservatism" traits are also very rare, except in the Vovnigi-2 sample, where this dental complex is almost as strongly pronounced as in the Upper Paleolithic Europeans.

Conclusions

The distribution and variation of dental nonmetric traits in the Mesolithic and Neolithic samples of the Russian Plain describe its population history as a complex process governed by many factors. There is solid evidence pointing towards a migratory influx from the East at the time of the Onega culture, or even earlier. The dental complex of the migrants included increased frequencies of shoveling, distal trigonid crest, and six-cusped lower molars accompanied by an increased robustness of mandibular second molars.

But the hypothesis about persistence of an autochthonous "evolutionarily conservative" dental complex, arising in the local Upper Paleolithic population in some Mesolithic and Neolithic groups, is supported as well. The highest prevalence of that complex is observed in the samples of the Onega Mesolithic culture and the Azov-Dnieper Neolithic culture, while some isolated "evolutionarily conservative" traits are found in the samples representing Kargopol and Ryazan variants of the Pit-Comb Ware culture.

The simultaneous presence of Mongoloid and "evolutionarily conservative" markers at Yuzhny Oleniy

Ostrov means that the long-term persistence of the Upper Paleolithic morphology in this group was not a result of biological isolation. This, in turn, makes it unlikely that undifferentiated dental complexes could have emerged simply as a result of genetic drift. As migration from the East did not lead to complete the disappearance of the "evolutionarily conservative" dental complex in the population of the North of the Russian Plain, it is plausible that such a conservation of ancient Upper Paleolithic morphology was due to its adaptive significance. The "erosion" of that complex was, rather, driven by the dispersal of post-Paleolithic groups across the Russian Plain, which led to the loss of some genetic lineages at the periphery of their areals.

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Received February 13, 2015.
Received in revised form May 4, 2016.