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AN UPPER PALEOLITHIC MANDIBLE FROM LISTVENKA, SIBERIA: A REVISION*

The mandible of a child from the Upper Paleolithic site of Listvenka in the Krasnoyarsk-Kansk forest-steppe, south-central Siberia, was subjected to a new detailed study. It was found in 1992 and was first published five years later with very incomplete information about place and context. The need for revision was prompted by the sophistication of dental trait batteries, new views of the diagnostic significance of certain dental traits, availability of new techniques, etc. Now the find can be related to habitation layer 12d, consistently dated to ca 13 ka on the basis of three estimates. Results of the multi-slice computed tomography suggest that the child was 3.5–4.5 years old. Like most fossils representing early anatomically modern humans, the specimen is rather robust by modern standards. Based on the combination of nonmetric and metric traits, the individual's place among other eight Upper Paleolithic children was assessed. The distinctive feature of the mandible is generally modern morphology combined with robusticity and a neutral position on the west-to-east scale. We tentatively describe this trait combination as Upper Paleolithic Central Siberian.

Keywords: *Upper Paleolithic, Listvenka, Siberia, dental anthropology, multi-slice computed tomography.*

Introduction

In August 1992, a human mandible was found at Listvenka—a stratified Upper Paleolithic site in the Krasnoyarsk-Kansk forest-steppe, south-central Siberia. For certain reasons, the first brief publication of the find appeared only in late 1997, and a more detailed publication, in 2001 (Shpakova, 1997, 2001). Both were authored by E.G. Shpakova, a Novosibirsk dental anthropologist who knew neither the context of the find nor even its exact location. This information was provided in a small article by E.V. Akimova (1998). Later, it was included in a detailed monographic study of the site

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(Akimova et al., 2005). We take the opportunity to revise this highly informative fossil.

The Upper Paleolithic was the time when anatomically modern humans diverged into major geographic groups, and all human remains dating to that period are relevant to that differentiation. In this study, we try to assess the taxonomic status of the mandible and provide its biological description with regard to the modern norm. Dental traits are subdivided into several groups according to their relevance to various aspects of the study.

Methods

To evaluate the morphology of the teeth we used the multi-slice computed tomography (MSCT) method (Vasiliev et al., 2011). For that purpose, we employed the Philips Brilliance-64 CT under Extremity and Sinus Volume modes.

The morphological description of the mandible focuses on the chin, especially its basal part, and nonmetric traits of the inner and outer relief with regard to taxonomic status, specifically to markers of anatomical modernity. The analysis of measurements focuses on robusticity indexes of the alveolar part.

Dental traits are those traditionally used by Russian anthropologists for evolutionary studies and for revealing dental differentiation within the modern human species (Zubov, 1968, 1974, 2006).

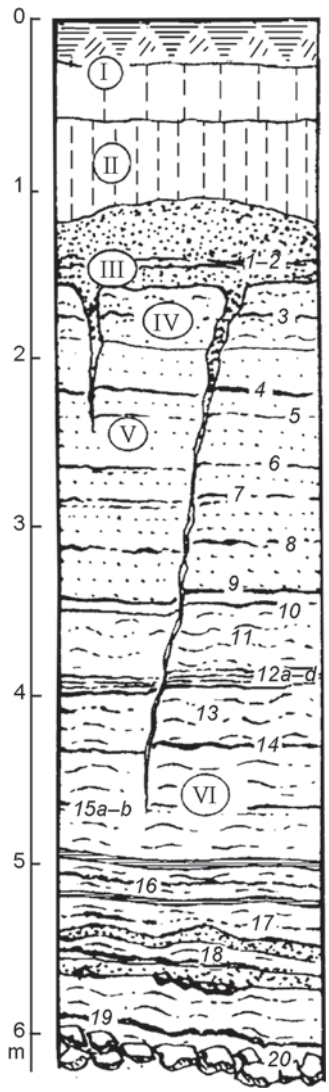

Fig. 1. Listvenka: a stratigraphic profile.
Roman numerals denote geological layers, Arab numerals, habitation horizons.

Archaeological context

Listvenka is a stratified site situated within Divnogorsk, a town 40 km southwest of Krasnoyarsk, on the right bank of Listvenka-Zarechnaya—the right tributary of Yenisei. It was discovered in 1982 by K.V. Zyryanov and excavated in 1983–1986 by a joint expedition from Krasnoyarsk Pedagogical Institute (since 1992, a University), and from the Institute of History, Philology and Philosophy SB RAS (since 1992, Institute of Archaeology and Ethnography SB RAS), headed first by N.I. Drozdov (1983–1986) and then by E.V. Akimova (1987–1997). Regular accounts of the findings were published (Akimova, 1992, 1996, 1998), resulting in a monograph (Akimova et al., 2005).

During the 1985 season, a layer (No. 12 by general numeration), weakly marked by carbonized organic inclusions and isolated tools, was identified (Fig. 1). This horizon comprised six thin weakly eolian substrata. The transect revealed their rhythmic wave-like distribution, splitting, fading, and eventual discoloration.

Five years later, work at the additional "southern" excavation revealed at least four independent habitation layers (12a–d), partly deformed and displaced, but mostly preserving their original position.

The most informative of these is layer 12d (Fig. 1). It contained a series of hearths, whose walls were paved with stone (flat boulders of plagiogranite were placed in an upright position along the high vertical sides of the pit) or without pavement (three equally sized small hearths arranged in a line). In the same layer, a mammoth ivory rod, having no parallels in Siberia, was found. Three consistent radiocarbon estimates were obtained for this layer: 13,100 ± 410 (GIN-6965), 13,470 ± 285 (SOAN-3733), and 13,910 ± 400 (SOAN-3833) BP.

The human mandible (Fig. 2) was discovered in square 21-E of layer 12d, at the mouth of a cryogenic crack. No artifacts or faunal remains were found in that area. The preservation of the mandible is similar

Fig. 2. The Listvenka mandible: general view.

to that of other bones from layer 12d. The crack ran along a small depression that gently sloped in the western direction. Similar forms of relief were traced in overlying levels. The mandible had apparently been scoured from an adjacent level and redeposited. Its original location may have been situated more easterly, immediately near the edge of the rock outcrops. No other human remains were found in any of the habitation horizons.

Multi-slice computed tomography

A series of CT slices (Fig. 3) was cut through the mandibular corpus (angles and rami had been destroyed post mortem). There is a likewise postmortem fracture in the left part of the chin and corpus at the mental foramen level without further destruction of bone.

The following teeth are present: 7.1 (left deciduous central incisor), 7.2 (left deciduous lateral incisor), 7.3 (left deciduous canine), 7.4 (left deciduous first molar), 7.5 (left deciduous second molar), 3.6 (left permanent first molar), 8.1 (right deciduous central incisor), 8.2 (right deciduous lateral incisor), 8.3 (right deciduous canine), 8.4 (right deciduous first molar), 8.5 (right deciduous second molar), 4.6 (right permanent first molar).

Teeth Nos. 7.1 and 7.2 are completely mineralized. The latter tooth is rotated at 45° and slopes distally. Both incisors are displaced downward, and the alveoli and underlying bone structure are damaged. Germs of permanent teeth are missing, but there is a postmortem bone defect that follows the contour of germs and coincides with the fracture line.

Tooth No. 7.3 is in the dental row, and no evidence of root resorption is present. The germ of the permanent

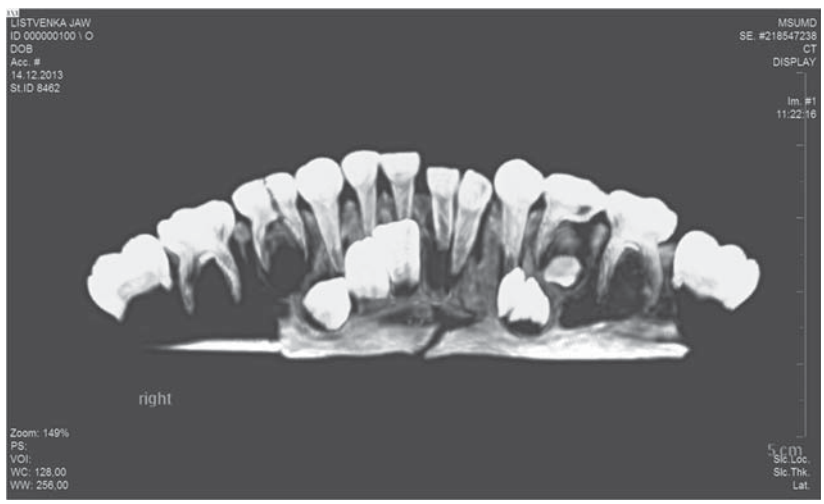

Fig. 3. Multi-slice computed tomographic image of the mandible.

canine No. 3.3 is in the final stage of crown calcification; its position is not changed. At that level, on the oral side, inside the cortical layer of the oral cortical plate, there is a germ of an additional tooth (a mineralized crown).

The distal root of tooth No. 7.4 is missing. The germ of the permanent molar No. 3.4 is situated inside the bone tissue, its crown is in the mineralization stage, and is turned down and orally.

Teeth Nos. 8.1 and 8.2 are in the dental row and show no traces of root resorption. Germs of permanent incisors Nos. 4.1 and 4.2 are inside the bone, their position is regular, and their crowns are formed.

Tooth No. 8.3 is in the dental row, evidencing no traces of root resorption. The germ of the permanent canine No. 4.3 is inside the bone, its axis is sloping medially at 45°, and the crown is mineralized.

Tooth No. 8.4 is in the dental row and shows traces of root resorption. The germ of the permanent molar No. 4.4 is missing, but the shape of the postmortem bone defect suggests that the germ was present. The fracture line passes through the place where it was, and tooth No. 8.4 is fractured along the longitudinal axis.

Teeth Nos. 7.5 and 8.5 are situated in the dental row. There are no traces of mineralization of crowns of permanent teeth at that level.

Teeth Nos. 3.6 and 4.6 are in the eruption stage (one half of the crown in the dental row), their crowns are completely formed.

Mandibular morphology

According to a classification by H. Schulz (1933), the anterior part of the mandible is of type 6, showing a pronounced triangular mental protuberance. Upper Paleolithic people display all variants except 1 and 4, but type 2, also characterized by a triangular chin with a mental protuberance (Vasiliev, 1999: 74), is the most frequent.

In terms of morphology of the basal part, most Pleistocene humans exhibit variants 3 and 6, marked by an overhanging chin. In Neanderthal mandibles, however, there is usually one point of support, whereas in those of *H. erectus* and *H. sapiens*, there are two such points (Gerasimova, Vasiliev, 1998: 113). The basal part of the Listvenka specimen is close to variant 6.

In all Pleistocene humans, the inner mandibular relief is more expressed than the outer relief, certain variations notwithstanding. The Listvenka mandible, like other Upper Paleolithic specimens, shows a marked lateral eminence. Both the marginal and the lateral tori as well as the furrow between them are faintly developed. The digastric fossa is marked.

Table 1. **Mandibular indexes**

Specimens	Robusticity index	Basal to alveolar parts ratio
Listvenka	0.69	0.73
Markina Gora	0.46	0.91
Cro-Magnon	0.54	1.30
Fish Hoek	0.54	0.77

The metric characteristics of the mandible are as follows (all dimensions are in mm):

Corpus height at second molar level, left	17.2
Corpus thickness at second molar level, left	11.8
Corpus height to mental foramen, left	8.1
Thickness of basal part at mental foramen level, left	11.6
Thickness of alveolar part at mental foramen level, left	8.5
Alveolar arch length from distal surface of second deciduous molars	27.4
Intercanine breadth (direct distance between outer surfaces of alveoli at mid-canine level	30.2

In sum, the mandible is rather large for a 3–4-year-old child. However, corpus height at the second molar level, height to mental foramen, alveolar thickness, and intercanine breadth show approximately the same means and variances in virtually all comparable specimens relating to Pleistocene *Homo* (Vasiliev, 1999: 87). In other words, they appear to be stable at the generic level.

Because absolute dimensions prove uninformative in this case, we compared the indices of the Listvenka mandible with those of other Upper Paleolithic mandibles (Table 1). As it turns out, the specimen is rather robust even compared to mandibles of adult individuals. The second index, however, testifies to a relatively gracile alveolar part, linking the Listvenka mandible with that from Fish Hoek.

Dental analysis

The first study of Listvenka teeth was done by Shpakova (1997, 2001). Our analysis is based on the revised nonmetric and metric data.

Nonmetric traits. According to Ubelaker's standards, the child's age should be estimated at 2–3 years (Ubelaker, 1987). However, age estimates based on the outward morphology of teeth are usually below those based on other trait systems or on science-based methods (Zubov, 2004a: 181). In this case, the MSCT pattern is consistent with standards for age of 3.5–4.5.

Russian dental anthropologists have traditionally subdivided traits into categories in terms of their informative potential. These categories include archaic, i.e., plesiomorphic and derived Neanderthal (Zubov, 1968: 56–65; 1974, 1984, 1999, 2000, 2004a, b, 2006; Khaldeyeva et al., 2008, 2010; Khaldeyeva, 2010; Bailey, 2002, 2006a, b; Martinón-Torres et al., 2006); derived modern and related to reduction; and those relevant to modern dental differentiation, i.e., western/Caucasoid, eastern/Mongoloid, and "relict", i.e., neutral with regard to the west-to-east gradient and possibly preceding it (Zubov, 1968: 49; 2004a: 31). Isolated weakly expressed Neanderthal traits and their combinations can occur in other archaic taxa, but with low frequency. Based on that approach, archaic, modern, and transitional patterns were described.

Archaic traits of the Listvenka mandible include:

(1) paraboloid dental arch, somewhat broadening at the level of the erupting first permanent molars (M_1/3.6 and 4.6);

(2) considerable convexity of enamel (grade 2) on the vestibular surface of lower canines (7.3 and 8.3) and deciduous molars (7.4, 7.5, 8.4, and 8.5);

(3) straight/labial/labiodont occlusion (Lb);

(4) a single main ridge in the center of the lingual surface of both deciduous canines (7.3 and 8.3);

(5) a single system of marginal ridges on the perimeter of the lingual surfaces of deciduous canines including the cutting edge (7.3 and 8.3);

(6) highest expression (grade 4) of the molar tubercle (a derivate of cingulum) on the left deciduous second molar (m_2/8.5);

(7) a relatively deep anterior fossa below the continuous mesial marginal ridge of the same molar;

(8) high tubercular apices of that tooth partly connected by the marginal ridge along the perimeter;

(9) elements of the posterior fossa on the talonid of the right permanent first molar (3.6);

(10) trigonid larger than talonid on both M_1 (3.6 and 4.6);

(11) accessory encircling marginal ridges on the surface (med, hld, partially end) of the left M_1 (4.6);

(12) posterior fossa situated in the distal part of that tooth;

(13) highly differentiated occlusal surfaces, deep intertubercular fissures and secondary furrows, curved centripetally directed principal ridges on both M_1;

(14) well developed cingulum in the basal part of the vestibular and partly lingual surfaces of crowns of deciduous and partly permanent molars;

(15) marked curvature/convexity of enamel on the vestibular surfaces of incisors, canines, and deciduous molars;

(16) metaconid larger than protoconid on the second deciduous molars (7.5 and 8.5);

(17) continuous mesial marginal ridge connecting metaconid with protoconid, and relatively deep anterior fossa below it on these teeth.

Relict traits of the Listvenka specimen include:

(1) deflecting wrinkle of metaconid (dw) on both second deciduous molars (8.5 and 7.5);

(2) odontoglyphic variant 2end (fc) on the left m_2 (8.5);

(3) variant 2end (III) on the right permanent first molar (3.6) close to the central fossa (fc), as in Africans.

The latter two traits originated at the formation stage of the eastern and western dental metaraces, the western one retaining the early modern Euro-African pattern.

Neanderthal apomorphies of the mandible include

(1) anterior fossa and elements of the distal protoconid crest on the left second deciduous molar (8.5). This is a remnant of the Korenhof triad—a Neanderthal apomorphy, which, in the case of Listvenka, is quite faintly expressed;

(2) central tubercle on the hypoconulid side on the right permanent first molar (3.6).

Modern apomorphies of the specimen include:

(1) absence of dental arch flattening in the frontal incisor area (7.1, 7.2, 8.1, and 8.2);

(2) crown indexes of the permanent first molars (4.6 and 3.6—89.7 and 91.3, respectively) are below 100;

(3) the concavity of the lingual surfaces of the first and second incisors (7.1, 7.2, 8.1, and 8.2) is weak, and there is no lingual cusp;

(4) odontoglyphic variants 2prd (II) and 2end (IV) on the right deciduous second molar (7.5);

(5) variant 2prd (II) on the right M_1 (3.6).

Western/Caucasoid dental traits are as follows:

(1) variant 2end (IV) on the right m_2 (7.5);

(2) variant 1hyd (IV) on both permanent first molars (3.6 and 4.6);

(3) type 1 of contact between furrows 1med/1prd on fissure II;

(4) type 2 of contact between furrows 1med/1prd—point of 1med confluence with fissure II is higher;

(5) no shoveling on the isolated right upper permanent central incisor.

Eastern/Mongoloid traits include:

(1) odontoglyphic variants 2med (III) and 2end (fc) on the left deciduous second molar (8.5);

(2) variant 2med (III) on the right m_2 (7.5);

(3) variants 2med (III) and 2hyd (I) on the right permanent first molar (3.6);

(4) variant 2hyd on the left M_1 (4.6);

(5) crown form $M_1$6 on both molars;

(6) parallel course of furrows 1 and 2 on the entoconid (end) of m_2 (7.5 and 8.5).

Metric traits. Measurements of the Listvenka teeth were compared with world averages (Zubov, 2006: 9–33). The mesio-distal dimensions of deciduous teeth slightly exceed the modern norm (Table 2). The vestibulo-lingual

Table 2. **Measurements of teeth of the Listvenka mandible**

Dimension	i_1	i_2	c	m_1	m_2	M_1
			Right			
MD	5.0	5.5	6.1	9.1	10.8	11.5
VL	4.0	4.6	6.0	7.0	9.2	10.5
			Left			
MD	5.1	5.5	6.8	9.5	10.9	11.9
VL	4.1	5.0	5.5	7.1	9.5	10.5
World average (MD/VL)	4.5/4.2	4.7/4.5	5.6/5.0	8.1/7.3	10.2/9.1	11.2/10.4

diameter and crown height are mostly comparable to modern standards, suggesting macrodonty, according to Zubov's classification (Zubov, 1968: 98). In terms of vestibulo-lingual dimensions, permanent molars (3.6 and 4.6) fall into the "medium" category, showing a slight tendency toward reduction. Crown indexes of these teeth (left, 89.7, right, 91.3) are in the 90–100 interval and match modern standards (Ibid.).

We have compared Listvenka with other Upper Paleolithic mandibles such as Sungir 2, Pushkari 1, Kostenki XVIII, Abri-Pataud, Laugerie-Basse, Grimaldi, and Eshkaft-e Gavi. In three cases (Listvenka, Sungir 2, and Eshkaft-e Gavi), an additional analysis was carried out with a view to using new techniques such as MSCT, statistical approaches, and new comparative data (Table 3).

The position of fossils with regard to mesio-distal and vestibulo-lingual diameters of the lower permanent first molars is shown on the plot (Fig. 4). The status of Upper Paleolithic individuals is noteworthy from several points of view. Some of them, such as Sungir 2 (1), Abri-Pataud (28), Grimaldi (27), and Laugerie-Basse (26), display maximal or very high values of one or both these diameters. Others show minimal, small or medium values. These include Kostenki XIV/Markina Gora (5), Samarkand 1 (38), Malta 2 (37), Listvenka (35), Eshkaft-e Gavi (32), and Kostenki XVIII (3).

Notably, Listvenka, dating to 13,470 ± 285 BP (Gerasimova et al., 2007: 117), links up with Kostenki XVIII, which is much earlier (21,020 ± 180 BP) (Ibid.: 110), and with Eshkaft-e Gavi dating to 35,000 BP (Scott, Marean, 2009). These fossils share a combination of a large mesio-distal diameter and medium vestibulo-lingual diameter, indicating absence of mesio-distal reduction.

The situation with Samarkand 1 (38) and Malta 2 (37) is different: they show medium mesio-lingual diameter combined with small vestibulo-lingual diameter, testifying to reduction, also evidenced by a Neolithic sample from France (23), as well as by the Mesolithic fossil Sidelkino 1 (29). Grimaldi (27) and Laugerie-Basse (26) take extreme positions with large and very large mesio-distal and vestibulo lingual diameters.

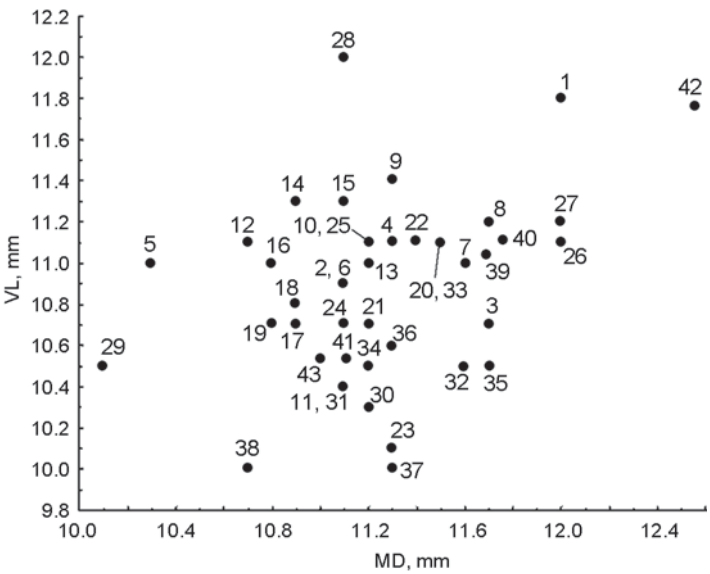

Fig. 4. Relationship between the mesio-distal and vestibulo-lingual diameters of the lower permanent first molar.
Figures refer to numbers of specimens and samples in Table 3.

Table 3. **Comparative measurements of M_1**

Nos.	Specimens	Source	MD	VL
1	Sungir 2	Zubov, 1984	12.0	11.8
2	Sungir 3	Same	11.1	10.9
3	Kostenki XVIII	Khaldeyeva, 2005, 2006	11.7	10.7
4	Upper Paleolithic, Western Europe	Trinkaus et al., 2003	11.3	11.1
5	Kostenki XIV/Markina Gora	Khaldeyeva, 2010	10.3	11.0
6	Late Upper Paleolithic, Western Europe	Frayer, 1977	11.1	10.9
7	Early Upper Paleolithic, Western Europe	Same	11.6	11.0
8	Fat'ma-Koba	Khaldeyeva, 2008	11.7	11.2
9	Murzak-Koba 1	Same	11.3	11.4
10	Murzak-Koba 2	″	11.2	11.1
11	Mesolithic, Yuzhny Oleniy Ostrov	Gravere, 1985	11.1	10.4
12	Mesolithic, Serbia	y'Edynak, 1989	10.7	11.1
13	Mesolithic, Ukraine	Jacobs, 1994	11.2	11.0
14	Mesolithic, southern Levant 1	Pinhasi et al., 2008	10.9	11.3
15	Mesolithic, southern Levant 2	Same	11.1	11.3
16	Mesolithic, southern Levant 3	″	10.8	11.0
17	Neolithic, southern Levant 1	″	10.9	10.7
18	Neolithic, southern Levant 2	″	10.9	10.8
19	Neolithic, southern Levant 3	″	10.8	10.7
20	Neolithic, Ukraine	Jacobs, 1994	11.5	11.1
21	Neolithic, Zvejnieki	Gravere, 1985	11.2	10.7
22	Neolthic, Poland	Szlachetko, 1966	11.4	11.1
23	Neolithic, France	Brabant, Twiesselmann, 1964	11.3	10.1
24	Neolithic, Britain	Brace, 1979	11.1	10.7
25	Neolithic, Vasilyevka	Zubov, 1968	11.2	11.1
26	Laugerie-Basse	Khaldeyeva et al., 2010	12.0	11.1
27	Grimaldi	Same	12.0	11.2
28	Abri-Pataud	Khaldeyeva et al., 2012	11.1	12.0
29	Sidel'kino 1	Zubov, unpublished	10.1	10.5
30	Caucasoids, modern	Zubov, 1968	11.2	10.3
31	World averages	Zubov, 2006	11.1	10.4
32	Upper Paleolithic, Eshkaft-e Gavi	Scott, Marean, 2009	11.6	10.5
33	Sidelkino 2	Zubov, unpublished	11.5	11.1
34	Chinese, modern	Zubov, 1968	11.2	10.5
35	Listvenka	Own data	11.7	10.5
36	Solovyina Luka	Shpakova, 2001	11.3	10.6
37	Malta 2	Zubov, Gokhman, 2003	11.3	10.0
38	Samarkand 1	Ibid.	10.7	10.0
39	Phum-Snay, Cambodia	Matsumura et al., 2011	11.69	11.04
40	Baikal, Neolithic	Matsumura et al., 2009	11.76	11.11
41	Epi-Jomon	Kaburagi et al., 2010	11.11	10.53
42	Malaisia, Middle Holocene	Matsumura, Hudson, 2005	12.56	11.76
43	Pleistocene, Altai (Okladnikov Cave)	Shpakova, 2001	11.0	10.53

The remaining Upper Paleolithic fossils such as Sungir 3 (2) and the Late and Early Upper Paleolithic samples from Western Europe (6 and 7) align with Mesolithic and Neolithic individuals, both diameters being large. Another subcluster consists of Mesolithic specimens (10, 12–16) having large vestibulo-lingual dimensions and medium mesio-distal dimensions.

In Neolithic individuals, which make up a separate subcluster, both diameters are medium to large. Other Neolithic samples (20, 22, 25, and 40) join Mesolithic and Upper Paleolithic fossils whereas others display smaller mesio-distal dimensions and a larger vestibulo-lingual diameter.

In Mesolithic teeth, the mesio-distal diameter is large and the vestibulo-lingual diameter, medium to large. The main factor responsible for similarities between Upper Paleolithic, Mesolithic and Neolithic samples appears to be gracilization (mostly relative reduction of the vestibulo-lingual diameter, as in Grimaldi and Laugerie-Basse, and absolute reduction of both diameters as well).

Dental pathology. Pockets around most teeth, porosity and roughness of the surrounding bone tissue attest to periodontal disease. On the lingual surface of the right deciduous first incisor (8.1) there is a pigmented spot below the cutting edge, near its distal corner. The lingual surface of the left deciduous second incisor (7.2) exhibits an enamel defect by being streaked with thin slightly pigmented grooves, which are also visible on the mesial surface, closer to the mesial angle of the cutting edge, where their loops encircle flat tubercles, some of which cluster into dense islands. A similar pattern (numerous tubercles densely spaced in a blackberry-like fashion) is observed on the distal/approximal surface of the left m_2 (8.5) crown. These may be signs of an inborn bacterial infection.

Conclusions

The MSCT pattern of the Listvenka mandible suggests that the child was 3.5–4.5 years old. The specimen is rather large for that age. It is no less robust than mandibles of Upper Paleolithic adults. Several morphological traits are typical of all Pleistocene humans, suggesting that they mark the genus *Homo* in general.

In some respects, however, the Listvenka mandible, like several other mandibles of Upper Paleolithic people, shows a tendency for gracilization, linking it to certain Mesolithic and Neolithic specimens characterized by a large mesio-distal diameter and medium or large (relatively reduced) vestibulo-lingual diameter of the lower permanent first molars.

As to the lower permanent first molars, Listvenka is characterized by the retention of certain archaic traits combined with modern apomorphies, and neutrality on the west-to-east (Caucasoid to Mongoloid) vector. Such a combination may testify to certain evolutionary conservatism with regard to both archaic, in fact Neanderthal, and evolutionarily younger relict traits. Tendency for reduction manifests itself in both metric and nonmetric features.

The Listvenka mandible may characterize a peculiar dental variety typical of the Central Siberian Upper Paleolithic and mirroring several evolutionary tendencies such as sapienization, incipient west-to-east differentiation between anatomically modern Eurasian groups, and reduction of certain dental dimensions. The overall impression is that of moderate evolutionary conservatism.

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