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Author(s): V. V. Pitulko, P. A. Nikolsky, E. Yu. Giryay, A. E. Basilyan, V. E. Tumskey, S. A. Koulakov, S. N. Astakhov, E. Yu. Pavlova and M. A. Anisimov

Source: *Science*, Jan. 2, 2004, New Series, Vol. 303, No. 5654 (Jan. 2, 2004), pp. 52-56

Published by: American Association for the Advancement of Science

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RESEARCH ARTICLES

The Yana RHS Site: Humans in the Arctic Before the Last Glacial Maximum

V. V. Pitulko,^{1*} P. A. Nikolsky,² E. Yu. Giryay,¹ A. E. Basilyan,²
V. E. Tumskey,³ S. A. Koulakov,¹ S. N. Astakhov,¹
E. Yu. Pavlova,⁴ M. A. Anisimov⁴

A newly discovered Paleolithic site on the Yana River, Siberia, at 71°N, lies well above the Arctic circle and dates to 27,000 radiocarbon years before present, during glacial times. This age is twice that of other known human occupations in any Arctic region. Artifacts at the site include a rare rhinoceros foreshaft, other mammoth foreshafts, and a wide variety of tools and flakes. This site shows that people adapted to this harsh, high-latitude, Late Pleistocene environment much earlier than previously thought.

The Berelekh site, at 70°N, dating to ~13,000 to 14,000 years ago (1), has long been accepted as the earliest evidence of humans anywhere in the Arctic (2, 3). Other Paleolithic sites in northeast Asia, including those in the Aldan River valley, lie far south of the Arctic Circle. Moreover, the dates for the oldest Aldan sites, ~32,000 to 33,000 years ago, as reported in the mid-1970s (4), are not universally accepted.

East Siberia was thus thought to have been colonized no earlier than 20,000 to 22,000 years ago. Some researchers believe the harsh glacial environment prevented human occupation of western Beringia until after the Last Glacial Maximum (LGM), about 18,000 years ago (5–7). Here, we describe a newly discovered, Paleolithic site on the Yana River, Siberia, at 71°N, that dates to 27,000 ¹⁴C years before present (¹⁴C yr B.P.) [about 30,000 calendar years (cal yr ago)] and discuss the implications for the peopling of this and adjacent regions.

The Yana River (Fig. 1) flows north for 879 km, first through sub-Arctic, then Arctic, regions, and empties into the Laptev Sea at 72°N. It is one of northeast Asia's largest rivers, with a basin of 238,000 km². Much of that basin lies within the Arctic Circle. In 1974, Scherbakova located nine Holocene sites between Verkhoyansk and the Yana-

Adycha junction along the Yana River (8). A decade later, nearly 70 Late Holocene sites had been found (9). However, several hundred kilometers of the Yana Valley, from the Yana-Adycha junction to the Arctic Ocean, remained largely unknown archaeologically. Little industrial activity occurred here.

The Yana RHS. In 1993, Mikhail Dashtzeren found a carefully worked foreshaft, with bevel ends (Fig. 2), made from the horn of a woolly rhinoceros (*Coelodonta antiquitatis*) in the Yana Valley. It bears a striking resemblance to Clovis foreshafts from North America (10–12). Surviving Clovis foreshafts are made from ivory. Rhinoceros horn, more flexible and less rigid, may have been more suitable than ivory. But rhinoceroses became extinct in Siberia about 14,000 to 15,000 radiocarbon years ago (13) and are not believed to have reached the New World. Presumably, Siberian hunters brought the technology of foreshafts with them when they entered the New World. Foreshafts permitted hunters to replace broken points quickly, then hurl the spear again—a great advantage when facing big game. Guided by Dashtzeren, we found a Paleolithic site in situ and named it Yana RHS. It occupies an ancient terrace on the river's left bank, at 70°43'N, 135°25'E (Figs. 1 and 3), about 100 km south of the current mouth (Fig. 1). At the site, ice-complex alluvial deposits form two terraces of different ages (14).

The higher terrace, formed by frozen silt with syngenetic ice wedges 4 to 5 m wide, rises to 40 m above the water line (a.w.l.). Because erosion is occurring at the top of the terrace, we use the water level as a baseline for all measurements. Radiocarbon dates place the age of this terrace at ~30,000 to 35,000 ¹⁴C yr B.P. Pleistocene bone remains collected in situ in the upper third of the

exposure date to >45,000 ¹⁴C yr B.P. (GIN 11697, bison; and GIN 11696, horse). Similarly, plant remains (peat) from 18 and 32 m a.w.l. date to >32,000 (LE 6027) and >29,000 ¹⁴C yr B.P. (LE 6002), respectively.

The lower terrace, which is frozen, rises to 16 to 18 m a.w.l. Its active horizon is no deeper than 0.7 to 0.8 m. The bottom layer is bedded sandy loam. At 12 m a.w.l., silt replaces loam. Terrace deposits include syngenetic ice wedges up to 2 m wide that form a polygonal grid. Polygons are relatively small, with a width on each side of 5 to 7 m. Here and there, second-generation ice wedges appear with widths reaching 0.5 m. The alluvial deposits contain numerous filiform rootlets and residues of twigs (or roots), plus isolated inclusions of allochthonous peat (Figs. 3 and 4). The upper part of the lower terrace also has a few lenses of Holocene lacustrine sediments 4 to 5 m thick that contain branches and tree fragments. Radiocarbon dates from these plant and tree remains vary from 3000 to 6700 ¹⁴C yr B.P. (Fig. 3).

The river now erodes this lower terrace. During our survey in 2001, we found four modern beaches with high concentrations of artifacts and broken and burnt bones along about 800 m of the river. The artifacts were most abundant on the roughly level inner edges of the beaches up

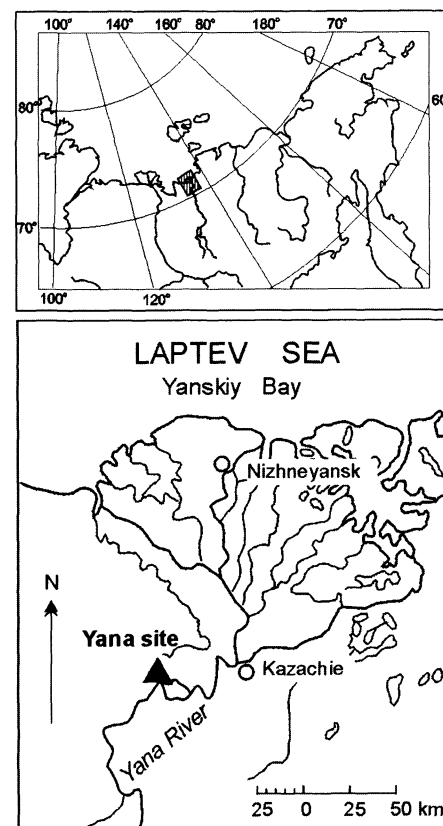


Fig. 1. Location map of the Yana RHS site.

¹Institute for the History of Material Culture, Russian Academy of Sciences, 18 Dvortsovaya nab., St. Petersburg 191186, Russia. ²Geological Institute, Russian Academy of Sciences, 7 Pyzhevsky pereulok, Moscow 119017, Russia. ³Geological Research Laboratory of the North, Faculty of Geography, Moscow State University, Leninskie Gory, Moscow 119992, Russia. ⁴Arctic and Antarctic Research Institute, 38 Bering Street, St. Petersburg 199397, Russia.

*To whom correspondence should be addressed. E-mail: archeo@archeo.ru, pitulko.volodya@nmnh.si.edu

Science

2 January 2004

Vol. 303 No. 5654
Pages 1–128 \$10



 AAAS

to 1.5 m a.w.l. In several places, cultural material appeared in talus just above the beaches with the highest abundance of bones and artifacts. Most of the beach material was covered slightly with sediment (Fig. 3).

On the modern floodplain, we found the remains of several collapsed frozen blocks of sediment. Some of these blocks evidently descended intact, holding units full of artifacts, diverse-sized flakes, and fragmented bones. Four radiocarbon dates were obtained from these bone fragments, excavated from a depth of 0.5 m in the floodplain (table S1).

Returning in 2002, we found at 7 to 8 m a.w.l. deposits of unevenly distributed arti-

facts and animal bones (including mammoth, bison, and horse), representing an in situ cultural layer within the lower terrace (TUMS1) (Fig. 4; figs. S1 to S3 and S5). We identified this same cultural layer (under the same geological conditions and at the same elevation) at three other exposures: TUMS2, AMA, and in a trench (Trench A) (figs. S4, S6, and S7). In that trench, the vertical distribution of the cultural material could be traced from concentrated surface finds at zero level, up the slope to 7.5 m a.w.l. No artifact lay at a higher level.

Geochronology. A horse mandible, associated with small bone fragments and stone flakes of varied size (fig. S8), was found in situ in a river bank cut at TUMS1. It lay at 7.5 m a.w.l. and dated $27,300 \pm 270$ ^{14}C yr B.P. (Beta 173067). These and other finds clearly marked an occupation level of 27,000 radiocarbon yr B.P., at 7 to 7.5 m a.w.l.: stratigraphically sealed within regular bedded silt accumulation, and retaining primary cryo texture.

The age of the occupation level was supported by a sequence of additional radiocarbon dates (standard radiometric), obtained from different elevations (Fig. 4, table S1). Elevations are given in meters above water level, from bottom to top, within the exposed area of TUMS1. At 6.75 m a.w.l., plant material (filiform rootlets) dated $26,500 \pm 600$ ^{14}C yr B.P. (LE 6443). At 7.5 m a.w.l., plant remains dated $25,900 \pm 750$ ^{14}C yr B.P. (LE 6444). At 8.3 m a.w.l., twigs dated $18,100 \pm 340$ ^{14}C yr B.P. (LE 6445). At 9.6 m a.w.l., plant remains (filiform rootlets) dated $22,400 \pm 300$ ^{14}C yr B.P. (LE 6446).

All dates, except at 8.3 m, agree with their stratigraphic position. Inversion at 8.3 m a.w.l. is less important than the consistency of the other dates. Plant material samples (filiform rootlets, water-screened with filtered water) produce either average ages or ones slightly younger than the level from which they were collected. The two most

important dates (6.75 m and 7.5 m a.w.l.) overlap with the horse mandible date at a 2σ level of confidence.

Eight additional ^{14}C dates link the cultural layer, blocks excavated on the modern floodplain, and surface finds. Six relate directly to the cultural material (table S1). Four of these (15, 16) came from the eroded cultural layer near the western limit of the elongated amphitheater, formed on the banks by thermo erosion (Fig. 3). Two came from foreshafts. Two others are dates on bones of a brown bear and Pleistocene lion. Bone collagen was used in both the radiometric and accelerator mass spectrometry dating.

Four standard radiometric dates were obtained from bones found on the floodplain (Secondary Context). The youngest is $25,800 \pm 600$ ^{14}C yr B.P. (GIN 11465). Three others are $27,800 \pm 500$ ^{14}C yr B.P. (GIN 11464), $27,400 \pm 600$ ^{14}C yr B.P. (GIN 11466), and $27,600 \pm 500$ ^{14}C yr B.P. (GIN 11467). GIN 11465 was run on a partly burnt piece of mammoth ivory. Sample GIN 11467 is a horse bone containing an embedded flake, together with a patch of gray silt, the parent material of the cultural layer. The material, used for the two other GIN dates, as well as all bone fragments that were radiocarbon dated, bore clear utilization, butchering, or cooking marks (table S1).

The rhinoceros foreshaft, one of two ivory foreshafts, and a horse mandible were dated by accelerator mass spectrometry. The rhinoceros foreshaft dates $27,440 \pm 210$ ^{14}C yr B.P. (Beta 162233). One of the two ivory foreshafts dates $28,250 \pm 170$ ^{14}C yr B.P. (Beta 173064). Both dates come from surface finds, as do dates from the Pleistocene lion and brown bear.

The date for the horse mandible lies between that of the Pleistocene lion, $26,050 \pm 240$ ^{14}C yr B.P. (Beta 173066), and that of the brown bear, $28,280 \pm 300$ ^{14}C yr B.P. (Beta 173065). This helps to estimate the age of the

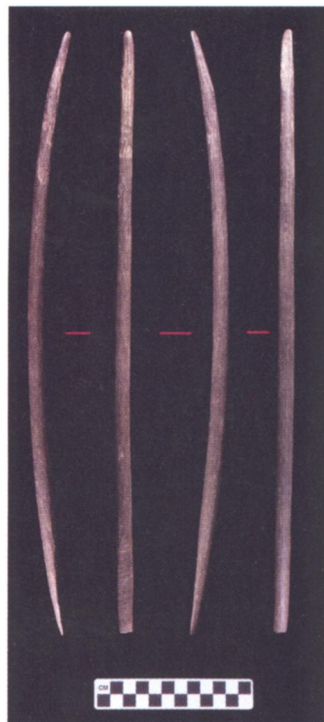


Fig. 2. Woolly rhinoceros foreshaft found by Dashtzeren in 1993.

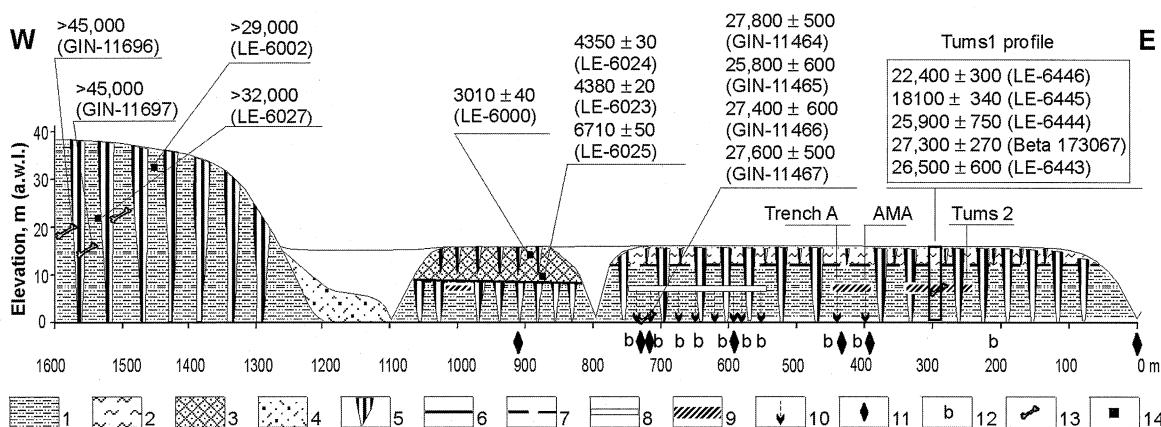


Fig. 3. Stratigraphy of the Yana River left bank bearing cultural deposits: (1) loamy sand; (2) silty loam; (3) organic partings-silty-sandy loam alternation strata; (4) contemporary slope and proluvum-alluvium deposits; (5) ice-wedges; (6) clear contact line; (7) gradational contact; (8) suggested presence

of the cultural level; (9) observed position of the cultural level at 7 to 7.5 m a.w.l.; (10) direction of transportation of archaeological material eroded from the cultural layer, and concentrations of it; (11) artifacts; (12) broken bones; (13) dated bone material; (14) dated plant, wood, and peat material.

surface bone collection (17). The date of the horse mandible alone links that collection to cultural level.

No contradiction occurs between the ^{14}C dates of the cultural layer, secondary context, and surface finds. Four dates fall within 400 years of each other and overlap at a 1σ level of confidence. Almost all overlap at a 2σ level of confidence. The coherency and consistency of dates suggest the site was occupied $\sim 27,000$ radiocarbon yr B.P. (about 30,000 cal yr ago).

Stone industry. During 2001 and 2002, we collected 376 artifacts of flinty slate, 1 object of granite, and 6 of quartz. Slate and granite occur in the riverbed. The quartz evidently came from elsewhere. More than 90% of these artifacts were on the beach as redeposited "surface finds," although some were covered by sediment. Flake scars on all flinty slate artifacts are well preserved. No object bears traces of rolling or river erosion.

We have not yet found any formal tool from the cultural layer. However, the cultural

layer in the TUMS1 profile (Fig. 4) yielded flakes ($n = 73$) and bone fragments ($n = 47$), differing in size, the smallest being 2 to 3 mm. Small pieces of red ocher were also found. The flakes, bone fragments, and ocher were recovered by water screening (figs. S8 and S9). Clearly, material in the cultural layer remained unsorted, in situ, as originally deposited some 27,000 years ago. No other cultural material along the riverbank, for a distance of 1.5 km, appears to be mixed. This suggests that Yana RHS is a single component site, representing a single, Upper Paleolithic stone industry.

The Yana RHS stone industry comprises unifacial and bifacial flaking of pebbles (siliceous slate) and nonpebble rocks (quartz crystal) (Fig. 5). Included are core-tools and flake-tools, with flakes (67%) as by-products of tool production. Some flakes were worked unifacially, many with ventral retouching. The remainder of the collection (33%, $n = 125$ pieces) was identified as tools. Major tool types include cores ($n = 27$); chopper and chopping tools ($n = 15$); bifacial and unifacial tools ($n = 36$), including pointed pieces; side and angle-scrapers ($n = 35$); end-scrapers ($n = 2$); chisel-like tools ($n = 2$); retouched flakes ($n = 7$); and a single hammer stone.

Berelekh, Dyuktai, and other sites of the Dyuktai culture do not relate to the Yana RHS industry and date considerably later (1, 4). No evidence of prismatic blades or wedge-shaped cores was found at Yana RHS. However, both Yana RHS and Berelekh site

have vast quantities of Pleistocene bones, especially mammoth bones. Both adjoin river crossings where big game could be trapped or often drowned when ice gave way.

Organic artifacts. The rhinoceros foreshaft measures 478 mm long (Figs. 2 and 6A). Its mid-diameter is 15 mm. It tapers slightly toward each end to 12 and 14 mm in diameter. Both ends are beveled on one side. This gives each end a half-round cross section. The angle of each bevel is asymmetrically offset with respect to the center line of the shaft.

At present, this foreshaft is slightly curved, probably due to the residual imprint of the parent material. During manufacture, it may have been straightened with a shaft wrench, combined with soaking, steaming, and/or heating. Morphologically similar specimens, but made from mammoth or mastodon ivory, are known from a handful of early sites in North America (10–12).

Two foreshafts of mammoth ivory, one complete, one fragmentary, were also recovered. Both were associated with stone tools and broken bones. Each is shorter than the rhinoceros foreshaft, but has the same shape, diameter, and width, in addition to the beveled ends. What appears to be a punch or an awl, made from a wolf (*Canis lupus L.*) metatarsal (Fig. 6B), was also found. Its distal end was not recovered, but what remains is 89 mm long, indicating a large animal, but within the range of modern wolves. Deliberate cuts on the bone may have kept a wrap in place, while the wrap, over time, burnished the bone.

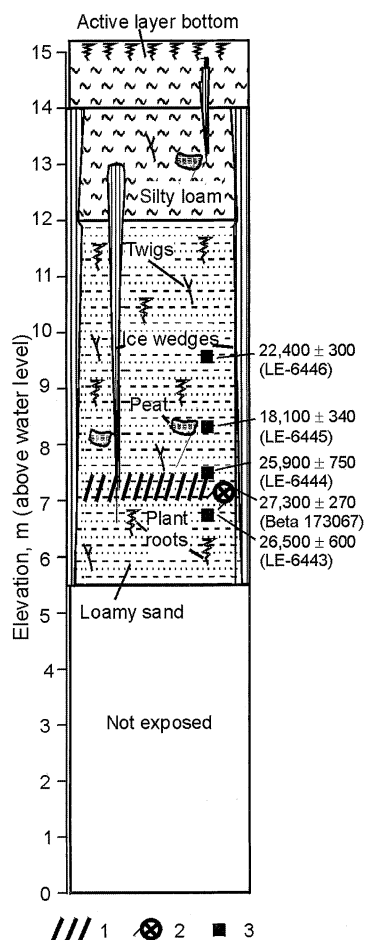


Fig. 4. Stratigraphy observed from TUMS1 profile: (1) permanently frozen cultural level; (2) dated horse mandible found in situ in association with flakes and small bone fragments (primary context); (3) radiocarbon dates obtained for the profile.



Fig. 5. Stone artifacts from Yana RHS: (A) a side scraper with bifacially retouched working edge; (B) worked piece of quartz crystal; (C) end scraper; (D) pointed tool; (E) a side scraper with bifacially retouched working edge. (A), (C), and (D), siliceous slate; (B), quartz crystal; (E), chert.

Faunal remains. Nearly 800 bones and bone fragments were collected at the Yana RHS and along the riverbank (18). These included both identifiable and unidentifiable bones. About a third of those identified can be associated with the exposed cultural layer. Bones identified by element ($n = 28$), as well as small water-screened fragments ($n = 47$), were excavated from the cultural layer, together with the artifacts. The others were simply gathered along the riverbank, both upstream and downstream from the site, for 1500 m.

On the basis of their potential relation to the cultural layer, these materials are grouped as follows: (i) bones and bone fragments discovered in the cultural layer; (ii) bones and bone fragments from the talus and floodplain terrace below the cultural layer; (iii) concentrations found on the beach downstream of the exposed cultural layer; and (iv) bones and bone fragments with no relation to the cultural layer, or with very low probability of such a relation.

The primary context, or Context One, the cultural layer, contained mammoth (*Mammuthus primigenius* Blumenbach) bones collected directly from the cultural layer (from 7 to 7.5 m a.w.l.). These include a small skull fragment, small fragments of ivory (split pieces), a fragment of thoracic vertebra of a young animal, and fragments of long mammoth bones. A horse (*Equus caballus* L.) mandible fragment with teeth was also recovered and dated. They also include reindeer (*Rangifer tarandus* L.) mandible fragments with teeth, isolated teeth, as well as fragments of radii, calcanei, and vertebrae; two bison (*Bison priscus* Bojanus) phalanges and a scapulae fragment; and Pleistocene hare (*Lepus tanaisticus* Gureev) vertebra and metacarpal, plus fragments of scapula, humerus, and mandible. There is also a woolly rhinoceros (*Coelodonta antiquitatis* Blumenbach) tooth

fragment, plus several dozen ($n = 47$) small, unidentified bone fragments from the same cultural level. All large bones, and almost all small fragmented bones, show traces of scraping.

Bones and bone fragments were collected from the talus, floodplain, and beach. All these areas lay below and adjacent to the cultural layer. Presumably, many came from there, as evidenced by the following: (i) large accumulations of bones appeared only in locations where this cultural layer was exposed or was recently exposed; (ii) one bone, sent for dating, contained a small stone flake; (iii) stone artifacts accumulated in these same locales; (iv) some of the bones bore traces of scraping; (v) intact, cracked, or slightly fragmented bones would normally be found in these regions, whereas the overwhelming majority were broken into small fragments, yet bore no evidence of "rolling"; (vi) the same accumulations contained burnt bone fragments; and (vii) radiocarbon dates from these bones are close to those from the cultural layer (see above). In addition to the bones of mammoth, woolly rhinoceros, reindeer, horse, bison, and Pleistocene hare, we identified bones from six other species: musk-ox (*Ovibos moschatus* Zimmerman), wolf (*Canis lupus* L.), polar fox (*Alopex lagopus* L.), brown bear (*Ursus arctos* L.), the Pleistocene lion [*Panthera spelaea* (Goldfuss)], and a wolverine (*Gulo gulo* L.).

Context Two. About 260 bones and bone fragments (excluding numerous, unidentified, small and tiny bone fragments) were found under conditions where their relation to the cultural layer was evident. These represented 11 mammalian species (18), plus unidentified birds. Mammals included mammoth, rhinoceros, Pleistocene bison, horse, reindeer, musk-ox, wolf, polar fox, Pleistocene lion,

brown bear, and wolverine. Only the reindeer and wolf still inhabit this area. Wolverine and bear are occasionally reported along the coastal lowland. The others (mammoth, rhinoceros, bison, lion) became extinct in Siberia or no longer reside there (musk-ox, horse). The Arctic hare replaced the Pleistocene hare.

Contexts Three and Four are hard to distinguish. Over 540 bones were found on the beach, upstream and downstream from the exposed cultural layer. Presumably, some belonged to this cultural layer, but we cannot link them unequivocally. The number of intact bones in this collection is much greater than that in the cultural layer. The composition of species remains the same. These include also the musk-ox (*Ovibos moschatus* Zimmerman), wolf (*Canis lupus* L.), polar fox (*Alopex lagopus* L.), brown bear (*Ursus arctos* L.), and a wolverine (*Gulo gulo* L.). Only one species, the Pleistocene lion [*Panthera spelaea* (Goldfuss)], is not present in the cultural layer. A single lion shoulder bone was found after the water dropped in late September, not too far from where Dashtzeren found the rhinoceros shaft. This bone dates to $26,050 \pm 240$ ^{14}C yr B.P. (Beta 173066). Conceivably, this species inhabited the area contemporaneously with the site occupancy.

Bones from the site, and from the surrounding area, appear typical of the Late Pleistocene in this area. Mammoth bones are relatively common, possibly from human activity. Reindeer is the most common species directly in the cultural site and presumably served as the major game animal. Bird bones also were found only at the site. Those who camped here evidently hunted reindeer, horses, and birds.

Implications. For more than 100 years, archaeologists have speculated about human residents in the Arctic during Pleistocene times, but lacked confirming evidence. The Yana RHS provides that evidence. The record of Arctic sites is fragmented: Yana RHS at 27,000 ^{14}C yr B.P., Berelekh at 13,000 ^{14}C yr B.P. (1, 4), and Zhokhov at 8000 ^{14}C yr B.P. (19). These time gaps need to be filled for a more complete understanding.

Formation of the cultural layer at Yana RHS coincides with the boundary between Kuranakh-Sala warming [the terminal stage of Karginsk/Middle Wisconsin (MW) Interval] and the Mus-Khaya cooling of Sartan/Late Wisconsin Glacial. The environment of the Yana delta then shifted from open, floodplain meadows to tundra. This part of Asia was never covered with large ice sheets. Average temperatures, reconstructed from pollen records, were colder than are those of today (20, 21). During Karginsk times, both landscape and climate varied in western Beringia (22). However, the environment remained favorable for large herbivores.

The extensive Bering Land Bridge formed during the Early Wisconsin Glacial (50,000



Fig. 6. Organic artifacts from Yana RHS: (A) the rhino horn foreshaft (proximal end); (B) wolf metatarsal bone (a broken awl?) with multiple cut marks; (C) cut marks (enlarged).

to 70,000 cal yr B.P.). It remained partly emergent during the warm Karginsk/MW Interval (23,000 to 50,000 cal yr B.P.). Paleo valleys of several major rivers (Lena, Yana, and others) can be traced on the Arctic shelf to a depth of 50 m at this time (23).

Yana RHS offers bifacial technology with no sign of blade making. By contrast, the Dyuktai culture combines bifaces with a blade industry based on wedge-shaped cores (3). Its earliest appearance in the Bering Land Bridge region dates to about 12,000 to 11,000 cal yr B.P. (24). Yana is 27,000 radiocarbon yr B.P. In theory, the Yana people may have crossed over the land bridge toward the end of Karginsk Interval.

It is difficult to assess similarities between Yana RHS and Clovis foreshafts. Thousands of kilometers and roughly 16,000 years separate them. Their similarity is intriguing, and they both have bifacial industries. Although a direct connection remains tenuous, the Yana RHS site indicates that humans extended deep into the Arctic during colder Pleistocene times.

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- Apparently, these terraces present Terrace 3 (the higher one, 35 to 40 m a.w.l.) and Terrace 2 (lower terrace, 16 to 18 m a.w.l.). Terrace 1 is not presented within the bluff. Presumably, it is totally eroded here. The floodplain terrace, or Terrace 0, exists here in the form of small sections.
- First ^{14}C dates for the site obtained by L. D. Sulerzhitsky (Geological Institute, Russian Academy of Sciences, Moscow).
- Species identification for ^{14}C samples provided by E. A. Vanghenheim (Geological Institute, Russian Academy of Sciences, Moscow).
- The Yana RHS bone collection offers the full range of carnivore species present at the end of the Karginsk Interval. Carnivore bones, especially those of the large species, rarely appear in natural exposures. The appearance of so many bones in one place suggests human activity in the past.
- Species identification provided by P. A. Nikolsky (Geological Institute, Russian Academy of Sciences, Moscow).
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- The Zhokhov-Yana Project, a long-term Russian-American effort, is directed by V. Pitulko and financed by a private foundation in New York. Unlim-

ited thanks to M. Dashtzeren, who guided us to Yana RHS; to the Lena-Delta Wildlife Reserve, Tiksi; to E. Savchenko, VICAAR (Victory Arctic & Antarctic Research, Ltd., St. Petersburg), for logistic skills; and to L. Sulerzhitsky (Geological Institute, Moscow), who provided ^{14}C dates when we were in the field. Unlimited thanks to the 28 people who, to date, worked at the Yana site.

Supporting Online Material

www.sciencemag.org/cgi/content/full/303/5654/52/DC1

Figs. S1 to S9

Table S1

2 April 2003; accepted 14 November 2003

Foxg1 Suppresses Early Cortical Cell Fate

Carina Hanashima,^{1,2} Suzanne C. Li,^{2*} Lijian Shen,³ Eseng Lai,² ††
Gord Fishell¹ ‡

During mammalian cerebral corticogenesis, progenitor cells become progressively restricted in the types of neurons they can produce. The molecular mechanism that determines earlier versus later born neuron fate is unknown. We demonstrate here that the generation of the earliest born neurons, the Cajal-Retzius cells, is suppressed by the telencephalic transcription factor *Foxg1*. In *Foxg1* null mutants, we observed an excess of Cajal-Retzius neuron production in the cortex. By conditionally inactivating *Foxg1* in cortical progenitors that normally produce deep-layer cortical neurons, we demonstrate that *Foxg1* is constitutively required to suppress Cajal-Retzius cell fate. Hence, the competence to generate the earliest born neurons during later cortical development is actively suppressed but not lost.

In both invertebrate (1, 2) and vertebrate (3, 4) central nervous system development, neuronal progenitors produce specific cell types in a characteristic temporal order. Analysis in the mammalian brain (5–7) and retina (8–10) suggests a general rule governing this process: Neural progenitors can produce cells characteristic of later but not earlier points in development. The mechanism behind this progressive restriction in progenitor potential is not understood. The laminar cell fate in the mammalian cortex provides an excellent model for studying these changes in progenitor potential. The mammalian cerebral cortex comprises six layers of neurons that are generated in an orderly

sequence during development (11, 12). With the exception of the Cajal-Retzius (CR) cells, which reside in layer 1, the cerebral cortex is produced in an inside-out manner. The deeper layer cells exit the ventricular zone (VZ) first, followed by more superficial cells at later periods. Hence, the birthdate of a cortical neuron is predictive of its fate (13–15). Furthermore, cell transplantation studies suggest that early-born classes of neurons can adopt later cell fates but not the converse (5–7). Thus, during cortical development, there appears to be a ratcheting mechanism by which the potential of early progenitors is progressively restricted.

The first restriction in the neuronal cell types that cortical progenitors can generate is the transition from the production of CR cells to the production of deep-layer neurons. CR cells, in addition to being the first postmitotic population, are of particular importance for the development of a properly organized cerebral cortex (16, 17). CR cells reside in the subpial region of layer 1 and secrete the extracellular glycoprotein Reelin (18, 19), which provides a critical signal for the guidance of later born cells that populate the cortical laminae. One of the few genes known to affect this early phase of cortical development is *Foxg1*, which encodes a winged helix transcriptional repressor (20–22). *Foxg1* controls the number of cells produced in the cortex and the loss of this gene results in hyp-

¹Developmental Genetics Program and the Department of Cell Biology, The Skirball Institute of Biomolecular Medicine, New York University Medical Center, 540 First Avenue, New York, NY 10016, USA.
²Cell Biology Program, Memorial Sloan-Kettering Cancer Center, 1275 York Avenue, New York, NY 10021, USA. ³Department of Physiology and Biophysics, Weill Medical College of Cornell University, New York, NY 10021, USA.

*Present address: Hackensack University Medical Center, 30 Prospect Avenue, Hackensack, NJ 07601, USA.

†Present address: Clinical Pharmacology, Merck Research Labs, RY34-A-428, 126 East Lincoln Avenue, Rahway, NJ 07065–0900, USA.

‡To whom correspondence should be addressed. E-mail: fishell@saturn.med.nyu.edu (G.F.); eseng_lai@merck.com (E.L.)