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Habitat conditions for *Camelus knoblochi* and factors in its extinction

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Abstract

The largest Eurasian camel *Camelus knoblochi* is known from Middle Pleistocene deposits of the Volga River Region and new material is described here. Its range included steppe and forest–steppe landscapes from Eastern Europe to the Transbaikalia in the Middle Pleistocene and from the Urals to northeastern China in the Late Pleistocene. The extinction of this species was related to climatic aridization and change of plant communities.

1. Introduction

Extended sandy and clayey beaches of the Volga River (from Volgograd to Saratov) are long known for numerous discoveries of large animal bones by local people (Poliakov, 1880; Cherskiy, 1888; Yakovlev, 1928). Considerable material of *Canis lupus*, *Mammuthus chosaricus*, *Stephanorhinus kirchbergensis*, *Elasmotherium sibiricum*, *Bison priscus longicornis*, *Saiga tatarica*, *Megaloceros giganteus*, *Cervus elaphus* from this area is preserved in museums and institutions of Russia and Kazakhstan (Pavlowa, 1926, 1931, 1933; Buinovskiy and Haveson, 1953; Gromova, 1965; Kozhamkulova,1981, 1986; Khromov et al., 2001a, b; Titov, 2006). Remains of a large camel are common among these fossils. Russian archaeologist and traveler Poliakov (1880) proposed to describe this large camel as *Camelus volgensis* based on the material found along the left bank of the middle reaches of Volga River on Khryazhevskaya and Krasnovidovskaya sandbars. However, this paper was never published. On the basis of a skull from the site Luchka in the Lower Volga Region, the new taxon *Camelus knoblochi* was characterized (Nehring, 1901). It was named in honor of Alexander Knobloch, the factory-owner from the town of Sarepta. He took a great interest in fossils and sent the skull with the lower jaw of this camel (presently the holotype) to the Zoological museum of St. Petersburg in 1880.

At present, most remains of fossil camels in the Volga Valley originate from the Middle Pleistocene Singil and Khazar alluvial deposits that are widespread in this region. These deposits are exposed in left bank cliffs in all places where animal remains were found.

Remains of *C. knoblochi* are known from several localities in the south of Eastern Europe (northern Caucasus, the Sea of Azov, Caspian, Middle and Lower Volga regions), in the east and west of northern Kazakhstan, as well as in Tajikistan, and the Altai Mountains, and in the south of western Siberia, southern and western Transbaikalia, and northern China (Fig. 1).

2. Systematic paleontology

Suborder selenodontia
Infraorder Tylopoda
Family Camelidae Gray, 1821
Subfamily Camelinae Gray, 1821
Tribe Camelini Gray, 1821
Genus *Camelus* L.
Camelus knoblochi Nehring (1901)

Abbreviations: GARM, Gorno-Altaysk regional museum, Gorno-Altaysk, Russia; GIN, Geological institute of Russian Academy of sciences, Moscow, Russia; IZK, Institute of Zoology of Kazakhstan Academy of Sciences, Alma-Ata, Kazakhstan; KHRG, Khvalynsk regional museum, Khvalynsk, Russia; PIN, Paleontological museum of Russian Academy of Sciences, Moscow, Russia; PM TSU, Tomsk state university, Paleontological museum, Tomsk, Russia; PRM, Pugachevsk regional museum, Pugachevsk, Russia; ROMK, Rostov-on-Don Regional museum, Rostov-on-Don, Russia; SRG, Saratov regional museum, Saratov, Russia; TsNIGR, Museum of All-Russian Geological Research Institute, St. Petersburg, Russia; VRM, Volgograd regional museum, Volgograd, Russia; ZIN, Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia.

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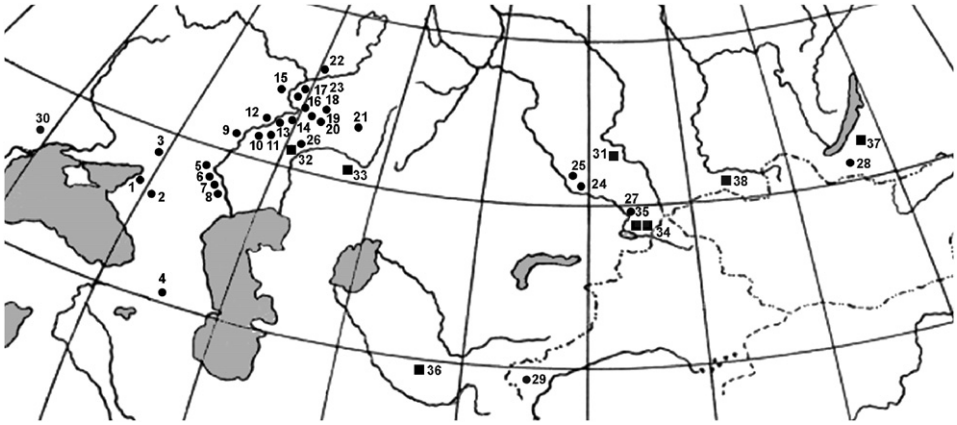

Fig. 1. *Camelus knoblochi* Nehring from Russia, Kazakhstan and Tajikistan. Round points—Middle Pleistocene localities; square points—Late Pleistocene localities. Middle Pleistocene: 1, Margaritovo; 2, Egorlyk; 3, Razdorskaya; 4, Leninakan; 5, Svetliy Yar (Luchka); 6, Raygorod; 7, Cherniy Yar; 8, Nikol'skoe; 9, Saratov (Sokolovaya gora); 10, Maliy Karaman; 11, Klopiha; 12, Khoroshevskiy island; 13, Voroniy island; 14, Smyshlaevka; 15, Sengiley; 16, Tungus peninsula; 17, Sobachiya prorva; 18, Sestra 1; 19, Ivanovka; 20, Kuzbaevo; 21, Trostian' island; 22, Laishevskiy capes; 23, Skripinky; 24, Irtysh; 25, Grigorievka; 26, Ural'sk; 27, Zyrianovsk; 28, Ust'-Kiran; 29, Lakhuti 2; 30, Tiraspol; Late Pleistocene: 31, Barnaul; 32, Rubezhka; 33, Ust'-Buhtarma; 34, Kamyshinka; 35, Martuk; 36, Samarkand; 37, Kamenka-1; 38, Izynzhul'.

Holotype: incomplete skull with lower jaw, Zoological museum (St. Petersburg, Russia), ZIN 8678.

Type locality: Luchka (nowadays Svetliy Yar town), Lower Volga Region, Russia.

Age of the type locality: Middle Pleistocene.

Material: 10 complete and fragmentary skulls, nine lower jaws, separate postcranial bones from several localities. Collections of GARM, GIN, IZK, KHRG, PIN, PM TSU, PRM, ROMK, SRG, TsNIGR, VRM and ZIN.

Description and comparison: the skull is relatively large (Table 1). The facial part of the skull is slightly elongated and makes up 59.8% of the basal length of the skull (specimen ROMK; Fig. 2). Nasals are short and relatively flat, their width is maximal at the base where they are 54–61% of their length. The anterior edge of the nasals is above the posterior third of the P3-C3 diastema. Premaxillary bones are large and unfused. The preorbital (ethmoidal) foramen is large. Nasal foramen is rather wide, its width amounts to 0.3 of its length. No facial crest is present. The ratio of the muzzle height to basal skull length is 20.7. Eye-sockets are closed and directed anterolaterally. The anterior edge of the orbit is located above the middle of M3 or between M2 and M3. The lachrymal vacuity is narrow and short. The palatine notch extends to the posterior border of M3. The maxillary fossa is subdivided into two parts, and is located above the anterior part of M1. The occipital crest is high, thin, and considerably overhangs the occipital bones. The sagittal crest is continuous, low and intersects the occipital crest.

Teeth are mesohypsodont. The tooth rows are nearly parallel to the sagittal plane of the skull, forming only a weak arch. The upper teeth include I3, C1, P1 and P3-M3 (Table 2). The small caniniform I3 is located laterally on the premaxillary bone. The canines are large, with an oval cross-section. Typically for adult males, the caniniform P1 is comparable with I3, and separated from the other premolars and the canine by long diastemata. There are sharp longitudinal ridges on the anterior and posterior edges of I3, C1 and P1. P2 is absent. On P3 the anterior valley is open. The P4 is molarized. Premolars and molars have ribs and strongly developed styles (especially the parastyle and mesostyle) on their labial surfaces.

The body of the mandible is low and inflated. The angular process is small, situated at the level of the tooth occlusal surface. The length of the symphysis is 0.3 that of the lower jaw. The angle between the horizontal and ascending rami varies from 100° to 105°. The p1 is caniniform; p2 and p3 are absent (Table 3). The p1–p4 diastema is about 54 mm long (specimen VSEGEI 7/2942). The lingual surfaces of the teeth are rather smooth except for weakly developed entostylids.

C. knoblochi is the largest species among known *Camelus* and *Paracamelus*. Bones of this species are the most massive in comparison with other Eurasian Camelidae. Metatarsals average slightly longer than metacarpals (Tables 4 and 5).

Compared to representatives of the genus *Paracamelus*, the Knobloch's camel differs in its more robust and larger limb bones, less elongated facial part of the skull, and absence of p3.

3. Stratigraphy, paleobiogeography and paleoecology

Neither the area nor time of origin of *C. knoblochi* is known at present. According to widespread opinion, Central Asia was the territory of the origin and dispersal of *Camelus*. Remains of *C. knoblochi* were found in the Early Middle Pleistocene Lakhuti 2 locality in Tajikistan (Vangengeim et al., 1988). Some isolated records of large camels with unclear stratigraphic position tentatively indicate the presence of this species in the Early Middle Pleistocene Tiraspol faunistic complex of Eastern Europe.

Table 1
Measurements of *Camelus knoblochi* skulls from several localities of European Russia

Measurements (mm)	Luchka ZIN, 8678 type	Razdorskaya ROMK	Saratov[a] SRG, 11187	Kvalynsk[a] KHRG, 1611	Sengiley VSEGEI, 7/2932
Maximal length	(660)[b]	590.0	–	–	–
Basilar length	(590)[b]	530.0	–	–	–
Cerebral cranium length	–	274.0	252.0	260.0	–
Facial cranium length	–	317.0	–	–	–
Anatomical length of cerebral cranium axis	–	197.0	158.0	155.0	–
Anatomical length of facial cranium axis	–	336.0	–	–	365.0
Orbital length of facial cranium	326.0	315.0	–	–	315.0
Maximal breadth in eye-socket level	(310)	271.0	–	–	298.0
Bizygomatic breadth	(300)	271.0	290.0	284.0	305.0
Maximal breadth of cerebral cranium	127.7	131.3	133.0	125.0	
Minimal breadth of cerebral cranium	106.0	100.4	93.0	110.0	
Breadth of facial cranium above foramen infraorbitalia	–	134.0	–	–	175.0
Minimal breadth above posterior diastema	(88)	74.0	–	–	75.3
Cranial height	–	–	150.0	143.0	–
Basioccipital breadth at the base of jugal processes	(210)	(182)	163.0	185.0	–
Breadth between auditory foramen borders	200.0	171.0	–	–	–
Parietal length	185.0	179.0	–	–	
Maximal nasalia breadth	–	69.3	–	–	(37)
Minimal nasalia breadth	–	55.0	–	–	(27)
Distance between the orbit and foramen infraorbitalia	107.8	76.8	–	–	97.0; 95.0
Occipital height from basion	137.0	128.0	131.0	140.0	–
Occipital height from opistion	93.4	90.4	–	–	–
Palatal length	–	330.0	–	–	343.0
Minimal palatal breadth	44.5	40.0	–	–	40.5
Nasal notch length	–	189.0	–	–	196.0
Nasal notch breadth in the middle	62.0	56.0	–	–	55.0
Anterior–posterior orbital diameter	74.0	66.0	–	–	70.0; 70.5
Vertical orbital diameter	67.0	64.0	–	–	60.0; 64.0
Occipital foramen height	47.7	34.0	–	–	–
Occipital foramen breadth	41.7	37.0	–	–	–
Length of diastema P1–P3	51.0; 49.0	87.0; 89.0	–	–	50.0
Length P3-M3	184.0	160.0; 170.0	–	–	196.0; 194.5
Length of diastema C1-I3	21.0	12.0; 10.0	–	–	–

Data in brackets—approximate measurements.
[a]Measurements from Khromov et al. (2001a).
[b]Measurements from Nehring (1901).

These finds are associated with localities of Tiraspol (Alexeeva, 1971) and Margaritovo (coll. PIN, 1325/15).

During the second half of the Middle Pleistocene, the range of *C. knoblochi* extended from the Sea of Azov Region to western Transbaikalia and included northern Caucasus, Middle and Lower Volga regions, Caspian Region, Kazakhstan, Tajikistan, Altai Mountains, southern West Siberia, southern and western Transbaikalia. It was the typical representative of the Singyl and Khazar mammal complexes of Eastern Europe and of the Samarov Fauna of East and West Siberia, and the Ust'-Kiransk Fauna of Transbaikalia (Vangengeim, 1977). This large animal coexisted with *C. lupus*, *M. chosaricus*, *S. kirchbergensis*, *E. sibiricum*, *Bison priscus longicornis*, *S. tatarica*, *M. giganteus*, and *C. elaphus*. *C. knoblochi* was typical during the Likhvin interglacial period. This camel probably became extinct in the territory of Eastern Europe during the onset of the Dneprovian (Moscow) Late Middle Pleistocene glaciation, due to the increasing aridity of this area.

The Late Pleistocene range of *C. knoblochi* shifted to Asia and stretched from the Urals to northeastern China (Kozhamkulova, 1986; Wei et al., 1998; Kalmykov, 1999; Tang et al., 2003). This large camel was the representative of the *Mammuthus primigenius-Coelodonta antiquitatis* fauna and its remains are found in some Late Paleolithic sites. Probably, the last *C. knoblochi* coexisted with *C. bactrianus*. During the Late Pleistocene, *C. knoblochi* became extinct and was replaced by *C. bactrianus*, a form more adapted for arid conditions established in Central Asia. Unfortunately, descriptions of Late Pleistocene camel remains are very scanty. Therefore, it is quite possible that some of the late records determined as *C. knoblochi* may actually represent *C. bactrianus*.

Many investigators assume that ancient camels, similar to their modern relatives, were exclusively dwellers of arid habitats. Very often, their presence in the fossil assemblage is interpreted as an indication of desert or semi-desert landscapes, high temperatures and deficiency of moisture.

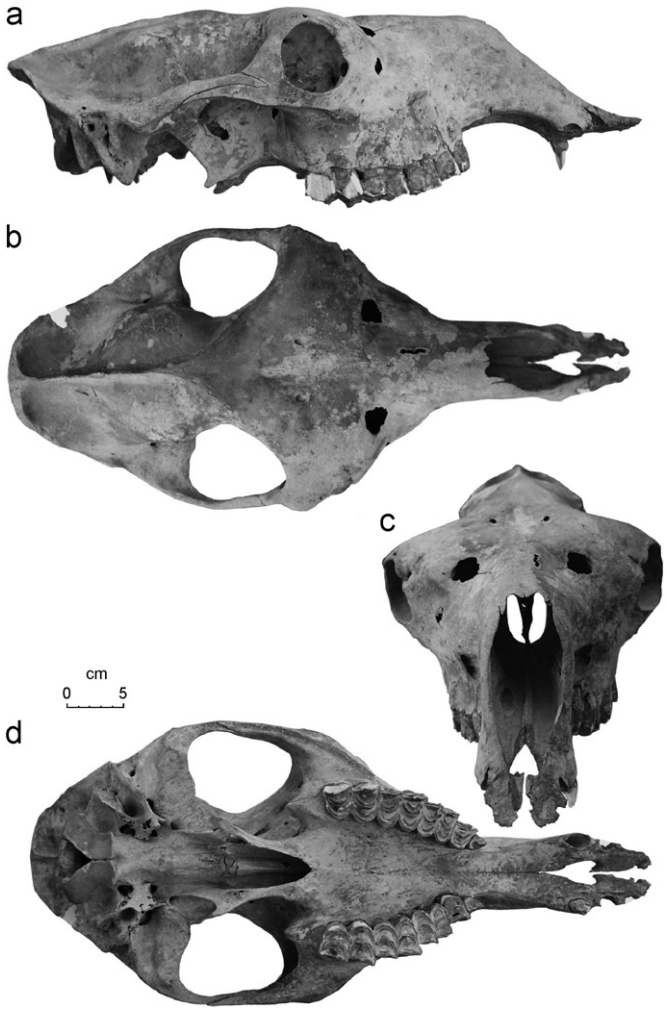

Fig. 2. *Camelus knoblochi* Nehring, skull from Razdorskaya site (lower reaches of Don River, Rostov Region, Russia; Middle Pleistocene): collection ROMK (without number) (a) lateral view; (b) dorsal view; (c) frontal view and (d) ventral view.

This extreme view is not warranted, but occurrence of the genus *Camelus* may have been connected with the spread of open landscapes in the territory of Eurasia. More competitive inhabitants of forest–steppes and steppes (such as large deer and ruminants) probably displaced camels from earlier customary habitats. The occurrence and mass expansion of camels happened at the end of the Pliocene through the beginning of Pleistocene. Early Pleistocene camels probably exploited open habitat but still thrived on relatively high quality vegetation. Later *Camelus* became restricted to lower quality habitat.

The accompanying animals indicate steppe and even forest–steppe environment for large fossil camels. Paleofloristic data show the existence of plant communities of steppe type combined with forested patches of oak, linden and other deciduous trees in the distribution area of this camel species (Grichuk, 1952). The association of small mammals of the Likhvin interglacial in the south of the Russian Plain also indicates the presence of forest–steppe conditions with the prevalence of steppe forms (Markova, 1992).

Table 2
Measurements of *Camelus knoblochi* upper teeth from several localities of European Russia

Measurements (mm)	Locality		
	Luchka ZIN, 8678 type	Razdorskaya ROMK	Sengiley VSEGEI, 7/2932
Length P3–P4	–	38.5; 39.2	–
Length M1–M3	140.0	123; 124	144; 142.3
Alveolar length C1	–	22.0; 23.1	–
Length C1	–	18.0	34.0; 37.0
Length I3	20.0	–	20.0
Width I3	15.0	–	16.0
Length P1	–	–	24; 23.2
Width P1	–	–	19.0; 17.0
Length P3	26.0	18.0; 18.7	28.0; 27.0
Width P3	25.5	17.0; 17.0	20.0; 22.0
Length P4	27.0; 28.0	22.4; 24.0	29.5; 31.0
Width P4	29.4; 29.0	27.1; 28.0	29.0; 29.3
Length M1	33.3; 31.0	34.3; 34.4	32.8; 33.8
Width M1	34.0; 33.0	33.0; 34.1	34.2; 34.2
Length M2	51.0	42.0; 41.6	54.3; 53.0
Width M2	38.0	36.6; 37.9	37.3; 35.3
Length M3	59.0	52.0; 52.7	61.4; 61.3
Width M3	35.0	36.1; 36.8	35.0; 25.0

Table 3
Measurements of *Camelus knoblochi* mandibles and lower teeth from several localities of European Russia

Measurements (mm)	Locality	
	Luchka ZIN, 4075, dex	Sengiley VSEGEI, 7/2932, dex
Length maximal	–	490.0
Length from the top of symphysis to end of m3	–	355.0
Length p4-m3	–	179.0
Length m1–m3	–	146.0
Length p1	–	17.0
Width p1	–	13.5
Length p4	–	28.0
Width p4	–	18.4
Length m1	–	31.5
Width m1	–	25.5
Length m2	43.0	49.2
Width m2	31.4	28.4
Length m3	73.0	72.0
Width m3	29.4	25.5
Symphysis length	–	148.5
Jaw height at p4	–	62.0
Jaw width at p4	–	33.7
Jaw height at m1	–	62.3
Jaw width at m1	–	38.3
Jaw height at m3	75.0	83.0
Jaw width at m3	45.0	49.5
Jaw height maximal	260.0	286.0
Length i_1–i_3	–	–
Alveolar length c1	–	48.0

Table 4
Measurements of *Camelus knoblochi* metapodiums from localities of Volga River Region

Measurements (mm)	Metacarpus coll. PIN[a]			Metatarsus coll. PIN, GIN[b], SRM[c]		
	n	Min–max	*M*	*n*	Min–max	*M*
Length maximal	4	397.0–418.0	408.75	3	391.0–421.0	406.7
Proximal end width	4	83.0–102.0	95.0	3	73.0–81.0	77.0
Proximal end anterior–posterior diameter	4	52.0–65.0	58.0	2	61.0; 59.0	–
Distal end width	3	133.0–136.0	134.0	3	92.0–108.0	101.3
Diameter at condyle divergence	4	24.0–32.0	28.75	1	30.0	–
Diaphysis width at midpoint	4	54.0–62.0	57.75	3	44.0–50.0	46.3
Diaphysis anterior–posterior diameter	4	43.0–51.0	48.25	1	55.0	–

[a]Measurements by Haveson (1954).
[b]Measurements by Alexeeva (1974).
[c]Measurements by Khromov et al. (2001b).

Table 5
Indices of slenderness of metapodials of some Camelinae (the ratio of distal end width to maximal length/the ratio of diaphysis width to maximal length)

	Paracamelus	*Camelus*		
	P. gigas Late Pliocene, China	*C. knoblochi* Middle Pleistocene Haveson (1954)	*C. bactrianus* Recent	*C. dromedarius* Recent
Metacarpus	–/(9.9)	31.1/13.65	26.8/10.9	25.45/8.2
Metatarsus	19.15/9.6	25.6/13.1	21.5/8.5	19.6/8.1

Adaptations to life in arid conditions, which were developed by modern camels, probably appeared later and were not characteristic for Plio-Pleistocene Camelinae. Wide and flexible alimentary adaptations of camels were the reason of their successful dispersal in conditions unsuitable for other herbivores. Taking into account that recent camels are perfectly adapted to conditions of steppes and forest–steppes, these animals do not inhabit these coenoses only due to intense competition with phyllophages and herbivores. It is probable that only the latest forms of camels developed adaptations to extremely arid situations.

It is possible that the biology of *C. knoblochi* resembled that of the recent *C. bactrianus ferus*. Even the modern camel has retained many characters typical for ancient forms, like a combination of a long neck and long legs, a rather long facial part of the skull, moderately hypsodont teeth. These features indicate the ability to feed in canopies, too. Recent feral camels prefer to feed on rather juicy and leafy vegetation, such as shrubby and subshrubby saltworts, onions, ephedra and young shoots of saxaul, leaves of poplar and reed. Despite their great endurance, wild camels nowadays suffer most of all from a reduced number of watering places. This was a principal cause of their area reduction in the past.

4. Conclusions

C. knoblochi was the largest Eurasian camel. Its stratigraphical range includes most of the Middle Pleistocene and Late Pleistocene. This species had its maximum distribution and highest abundance in the Late Middle Pleistocene, when its range extended from Eastern Europe to Transbaikalia. In the Late Pleistocene, *C. knoblochi* inhabited a considerable part of Asia from 39° to 54°N between the Urals and northeastern China.

Palynological data and paleozoological contexts indicate steppe and forest–steppe environments of the species. Most likely, *C. knoblochi* fed mainly on grassy vegetation. However, its diet also included sprigs and leaves. Their extinction was caused by climatic aridization during the Late Pleistocene accompanied by the drastic change of plant communities. In this climatic situation, camels were displaced to relatively extreme conditions of dry steppe and semi-deserts because of high competition with more efficient phyllophagous and herbivorous animals such as large deer and ruminants. Large *C. knoblochi* became extinct, being replaced by *C. bactrianus*, which is better adapted to severe environments and to feeding on less nutritious vegetation.

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