The pleistocene cave lion, *Panthera spelaea* (Carnivora, Felidae) from Yakutia, Russia

Gennady Baryshnikov and Gennady Boeskorov

Summary

Analysis of skulls and mandibles of the fossil Beringian lion demonstrate that the small lion that inhabited Yakutia (Russia), Alaska (USA), and the Yukon Territory (Canada) is a new subspecies described here as *Panthera spelaea vereshchagini* n. subsp. It differs from the European cave lion *P. spelaea* (terra typica: Gailenreuth Cave, Germany, Late Pleistocene) by its smaller size and from the American lion *P. atrox* (terra typica: Natchez, Mississippi, Late Pleistocene) by smaller size and by skull proportions.

Samenvatting

Uit een analyse van schedels en onderkaken van de fossiele leeuw van Beringië blijkt dat de kleine leeuw die in Yakutië (Rusland), Alaska (USA) en Yukon Territory (Canada) leefde een nieuwe ondersoort vertegenwoordigt, die hier beschreven wordt als *Panthera spelaea vereshchagini* n. subsp. Deze leeuw verschilt van de Europese grottenleeuw *P. spelaea* (terra typica: Gailenreuth grot, Duitsland, Laat Pleistoceen) door een kleinere lichaamsgrootte; hij verschilt van van de Amerikaanse leeuw *P. atrox* (terra typica: Natchez, Mississippi, Laat Pleistoceen) bovendien door andere schedelproporties.

Introduction

Fossil remains of a large *Panthera* from pleistocene deposits of the Siberian Arctic were first identified by Chersky (1891) who attributed them to *Felis* [=*Panthera*] *tigris* L., the modern tiger. This attribution was due to the difficulty of distinguishing osteologically between *P. tigris* and *P. leo*, the modern lion, and also to the fact that tigers in east Siberia have a northern distribution that reaches as far as the Aldan river in Yakutia (55° N) (Heptner & Sludsky, 1972). Later it was shown (Freudenberg, 1914; Riabinin, 1919, 1932; Gromova, 1932) that the fossil remains of large cats from Siberia belong to the cave lion, *Felis* [=*Panthera*] *spelaea* Goldfuss, well represented in pleistocene deposits in Europe (terra typica: Gailenreuth Cave, Germany; late Weichselian Glaciation). More recently, Vangengeim (1961), Vereshchagin (1971) and Boeskorov & Lazarev (1996) showed *Panthera spelaea* to have been widespread in eastern Siberia in the Middle and Late Pleistocene, when it ranged northward to the New Siberian Islands. Remains of a lion-like cat variously referred to *P. atrox* (Leidy) (Harington, 1969) or *P. leo atrox* (Harington, 1977, 1996) have also been found in the Yukon Territory. In addition, *P. atrox* (Harington, 1969) and *P. atrox alaskensis* (Frick, 1930) have been reported from Alaska. Elsewhere in late pleistocene North America *P. leo atrox* occurred southward beyond the Wisconsinan Glaciation boundary (terra typica: Natchez, Mississippi).

Vereshchagin (1971) thought the Beringian lion represented the Eurasian *P. spelaea* rather than *P. atrox*. Kurtén (1985) confirmed this view and showed that Beringian lions from Alaska and the Yukon Territory were on average smaller than European *P. leo spelaea*. He assumed that the size of the cave lion decreased northeasterly across its range, as a cline. In the past two decades, European paleontologists have usually treated the cave lion as a subspecies of *P. leo*, thus *P. leo spelaea* (Kurtén, 1985; Argant, 1991). In cave lion skull morphology, however, there are characteristics of both *P. leo* and *P. tigris* (Vangengeim, 1961; Rousseau, 1971; Vereshchagin, 1971). On the basis of brain structure, for example, the cave lion shows closer agreement with the modern tiger than with the modern lion (Groiss, 1996). This morphological mosaic points to the evolutionary distinctiveness of the cave lion. We agree with Vereshchagin (1971) that the unique specialized features of the Eurasian pleistocene cave lion, in which it differs from modern lions and tigers, distinguish it as a separate species, *Panthera spelaea*. We also view the American lion, *P. atrox*, as a distinct species (see also Turner, 1997).

Localities and Materials

Our characterization of *P. spelaea* from the Siberian Arctic during successive pleistocene stages and review of its systematic position is based on

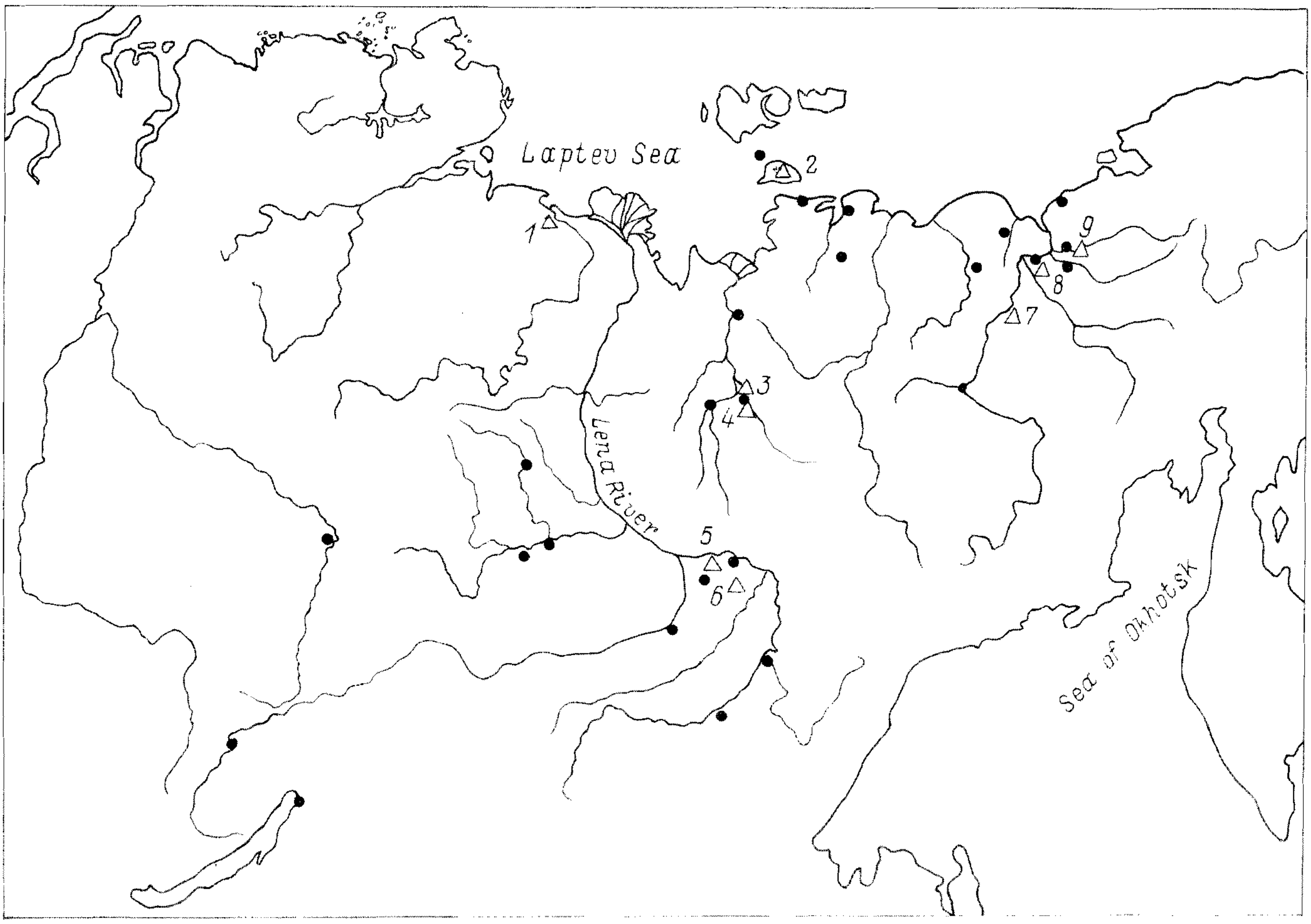

Fig. 1 Pleistocene localities with remains of *Panthera spelaea* in Yakutia. Open triangles mark discoveries mentioned in the text: (1) Mokhokho, (2) Bolshoy Lyakhovsky Island, (3) Kyra Sullar, (4) Ulakhan Sullar, (5) Oner Lake, (6) Ytyk-Kyuel, (7) Beresovka river, (8) Duvanny Yar, (9) Constantinovski Yar

Pleistocene vindplaatsen met resten van *Panthera spelaea* in Yakutia. Open driehoekjes duiden op vondsten die in de tekst genoemd zijn

the study of four skulls and seven mandibles from the collections of the Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZIN), Geological Institute, Russian Academy of Sciences, Moscow (GIN), Yakutian Geological Institute, Siberian Branch of the Russian Academy of Sciences, Yakutsk (YGI), and the Mammoth Museum, Yakutian Academy of Sciences, Yakutsk (MM). We also utilized measurements of two mandibles in museums in Ytyk-Kyuel and Bogorontsy, Yakutia (Boeskorov and Lazarev 1996).

Middle Pleistocene

Ulakhan Sullar, Adycha river (fig. 1). A fossilized left mandible (MM 6880) (fig. 2) from a spit in the Adycha river, near a locality containing fossils of *Equus (Plesippus) verae* Sher, *E. colymensis* Lazarev, *E. nordostensis* Russanov, and *Cervalces latifrons* Johnston (Lazarev & Tomskaya, 1987). Lacking evidence of transport abrasion, the

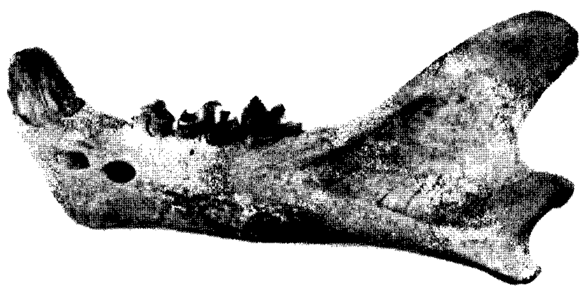

Fig. 2 Left mandible of *Panthera spelaea vereshchagini* n. subsp. from Ulakhan Sullar, the Adycha river (MM 6880), labial view

Linker onderkaak van *Panthera spelaea vereshchagini* n. subsp. (nieuwe ondersoort) van Ulakhan Sullar, Adycha rivier (MM 6880), wangzijde mandible may originate from this locality. In this case it is attributed to the Middle Pleistocene.

Berezovka river, Kolyma river. A fossilized right mandible (ZIN 31823) from the mouth of the Berezovka river, a right tributary of the Kolyma river. A skull of *Trogontherium cuvieri* Fischer (Vaskovsky, 1959) from the same locality indicates an age not younger than early Middle Pleistocene. It is unclear, however, if the *Panthera* mandible originates from the same stratum. A right mandible of a smaller lion (ZIN 29405) and a fragment of another small mandible (female?) (GIN 833-104) were also found at this locality. All these specimens are presumably of Middle Pleistocene age (see also Vereshchagin, 1971).

Late Pleistocene

Mokhokho, Olenek river. A well-preserved calvarium (ZIN 29398) (fig. 3) from the Olenek

Table 1 Size of skulls (in mm) in late pleistocene *Panthera spelaea vereshchagini* n. subsp. from Yakutia

Schedelgrootte in mm van *Panthera spelaea vereshchagini* n. subsp. , een nieuwe ondersoort uit het Laat Pleistoceen, Yakutia

Measurements	Males			Female
	Duvanny Yar, Kolyma River		Bolshoy Lyakhovski Island	Mokhokho, Olenek River
	YIG 6397 Paratype	YIG 3190/1 Paratype	ZIN 15572	ZIN 29398 Holotype
1		309.0		303.0
2	294.0	295.1		280.8
3	275.2	275.4		263.3
7	ca 150	162.0		177.1
8	143.0	148.0		147.5
9	134.5	140.5		133.8
10	125.2	126.0		118.1
11	157.0	155.0		146.8
C^1-P^4 L	102.0	102.7		99.4
13	69.3	64.3		71.4
16	47.0	47.1	47.3	42.0
17	29.8	28.0	34.0	27.9
18	122.0	125.6	150.1	124.2
19	64.0	60.8	67.9	61.7
23	212.0	213.8		198.1
25	59.1	61.0		58.2
26	123.3	120.8		118.7
27	91.4	88.0		87.0
28	66.0	61.4	55.6	59.8
29	91.4	88.0		87.0
30	66.0	61.4		64.5
32		95.3	95.4	90.3
Teeth:				
C^1 L	28.4	26.4		24.0
C^1 W	19.9	18.2		16.6
P^3 L	22.9	25.3		24.4
P^3 W	10.3	13.5		13.3
P^4 L	37.0	38.1		35.5
P^4 Lmts	13.3	14.4		13.4
P^4 W	17.2	17.3		17.5

Fig. 3 Skull of *Panthera spelaea vereshchagini* n. subsp. from Mokhokho, Olenek River (ZIN 29398). Holotype. Lateral (top), palatal (right), and dorsal (left) views

Schedel van *Panthera spelaea vereshchagini* n. subsp. (nieuwe ondersoort) van Mokhokho, Olenek Rivier (ZIN 29398). Holotype; hierop is de beschrijving gebaseerd. Diverse aanzichten: zijkant (boven), onderzijde (rechts) e bovenzijde (links) river, 15 km upstream from its mouth. The size of the calvarium is slightly smaller than in skulls known from Bolshoy Lyakhovsky Island and the Mokhokho specimen may belong to an adult female. The geological age of the fossil is most probably Late Pleistocene (Vereshchagin, 1971).

Bolshoy Lyakhovsky Island. A well-preserved but weakly fossilized neurocranial portion of a skull (ZIN 15572) is found near Maloe Zimovie. The geological context of the specimen is unknown but presumably consisted in Zyrianka Glaciation deposits of late pleistocene age that are widespread on the island. The same geological age is given to a right mandible (GIN 367/247) from the southern part of the island. It was found together with remains of other mammals contemporary with the late mammoth, *Mammuthus primigenius* (Vangengeim, 1961).The basal margin of the jaw is straight but the posterior margin of the coronoid process does not extend backwards farther than the posterior margin of the condyle process. The latter feature is typical of

Table 2 Geographical variability of basal length (in mm) of skulls of late pleistocene *Panthera spelaea* and *P. atrox* from the Holarctic

Geografische variatie in basale lengte (in mm) van schedels van *Panthera spelaea* en *P. atrox* van Holarctica, Laat Pleistoceen

Subspecies and localities	n	lim	x	N
P. spelaea spelaea				
Riss -Würm				
Binagady, Transcaucasia				
females (Vereshchagin, 1971)	1	248		
Würm/Wisconsinan				
Gailenreuth Cave, Germany				
males (Dietrich, 1968)	3	325-340	332.67	
female (coll. NHM)	1	270.5		
Arrikrutz, Spain				
male (Altuna, 1981)	1	339		
Europe and the Urals (Vereshchagin, 1971)				
males	6	300-335	323.20	12.21
females	5	266.7-304	290.66	14.33
Western Siberia				
male (ZIN 32745)	1	296.5		
female (ZIN 32607)	1	290.1		
Total: males	11	296.5-340	324.79	13.69
females	8	248-304	281.69	20.35
P. spelaea vereshchagini n. subsp.				
Yakutia (our data)				
males	2	275.2-275.4		
females	1	263.3		
Dawson, Yukon Territory				
female (Harington, 1977)	1	278.2		
Total: males	2	275.2-275.4	275.30	
females	2	263.3-278.2	270.75	
P. atrox				
Rancho la Brea, California (Merriam and Stock, 1932)				
males	10	338.9-404.7	359.00	21.56
females	8	269.0-321.9	297.40	19.60

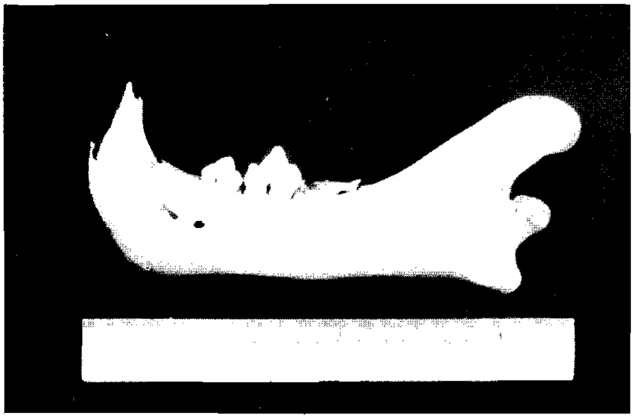

Fig. 4 Left mandible of *Panthera spelaea vereshchagini* n. subsp. from Ulakhan Sullar, Adycha river (private collection), labial view

Linker onderkaak van *Panthera spelaea vereshchagini* n. subsp. (nieuwe ondersoort) van Ulakhan Sullar, Adychá rivier (privé verzameling), wangzijde

P. leo and *P. spelaea* but not of *P. tigris*. The large size of the mandible indicates an adult male.

Kyra Sullar, Adycha river. A left mandible (MM 7315) from Kyra Sullar, several kilometres downstream from Ulakhan Sullar. Although the teeth are damaged to varying degrees, the specimen lacks evidence of stream transport. The projection of the chin is weakly developed and the coronoid process does not extend backwards to the posterior margin of the condyle process, as is typical of *P. leo*. Although adult, the mandible is of small size and probably female. Kyra Sullar contains deposits of early middle pleistocene to late pleistocene age. At various times in the past the bones of *Ursus arctos, Mammuthus primigenius, Equus nordostensis, E. orientalis, E. colymensis, E. lenensis, Alces alces, Rangifer* sp., *Cervalces latifrons* (?), *Bison* sp., and *Ovibos pallantis* have been recovered here. The geological age of the specimen is thus uncertain, but most probably late pleistocene.

Ulakhan Sullar, Adycha river. A left mandible (fig. 4) (private collection, unnumbered) from a sandy bank of the Adycha river. The canine and M_1 are broken; the P_3 and P_4 are nearly complete. Remains of *Equus lenensis* and *Bison priscus* cf. *occidentalis*, both commonly found in late pleistocene localities, were associated with the mandible. The mandible is of small size, which agrees with an immature individual. The basal margin is convex. The projection of the chin is prominent and the posterior margin of the coronoid process extends well beyond the posterior margin of the condyle process. These features are characteristic of the tiger, *P. tigris*, but the immature mandible of a young pleistocene lion is more similar to the tiger's mandible than it is to the mandible of an adult lion (e.g., Vereshchagin, 1971).

Oner Lake, Ust-Aldanski Ulus, Lena river basin. A right mandible (in the museum in Borogontsy) from late pleistocene shore deposits of Oner Lake. The specimen lacks evidence of stream transport. The jaw is short but massive. Height of the mandible beneath the P_4 is 47 mm. Projection of the chin is prominent and the basal margin of the jaw bears a small protuberance. The angular process is weak and deflected downward (Boeskorov & Lazarev, 1996). The specimen belonged to an adult animal, presumably a male.

Ytyk-Kyuel, Tattinski Ulus, Lena river basin. A left mandible (in the museum in Tatta) from near

Table 3 Factor score coefficients for the first two factors

Factor score coëfficienten voor de eerste twee maten

Measurements	Factor 1	Factor 2
2	0.970	-0.069
P^3 L	0.944	0.034
P^4 L	0.882	0.089
17	0.346	-0.922
18	0.930	-0.176
23	0.933	-0.185
25	0.927	0.220
27	0.916	0.173
28	0.832	0.299
Variance explained (in %)	76.169	12.189

the village of Ytyk-Kyuel, found at a depth of 3 m in late pleistocene deposits. The specimen lacks evidence of stream transport, which suggests that its occurrence was *in situ*. Like the Oner Lake mandible, projection of the chin is prominent and the basal margin of the jaw beneath the M_1 has a small protuberance. The mandible is similar to that of the tiger (*Panthera tigris* L.), but the large size of the M_1 suggests it is more readily attributable to a lion (Boeskorov & Lazarev, 1996). The teeth show light wear, as in prime adult individuals.

Duvanny Yar, the lower Kolyma river. Two lion skulls, YGI 3190/1 and YGI 6397, come from this locality. Both originate from a yedoma suite assigned to the second half of the Late Pleistocene. Both skulls lack evidence of stream transport. YGI 3190/1, which is well preserved, probably belonged to an adult male. Cervical vertebrae I - III, a thoracic vertebra and a metatarsus III, possibly from the same individual, were in association with the skull. A radiocarbon date of 36,000 ^{14}C yr B.P. (GIN-8327) was obtained for the thoracic vertebra. YGI 6397, which is more poorly preserved. This specimen is also evidently male.

Constantinovski Yar, Malyi Anyui river, Kolyma river basin. A mandible (GIN 836-295) of an adult male lion recovered from late pleistocene deposits.

Methods

For comparison of these Siberian materials we studied collections of European *P. spelaea* in the Zoological Institute in St. Petersburg, the Natural History Museum in London (NHM), and the Institute of Systematics and Evolution of Animals in Krakow (ISEA). In addition, we consulted data reported by Merriam & Stock (1932), Dietrich

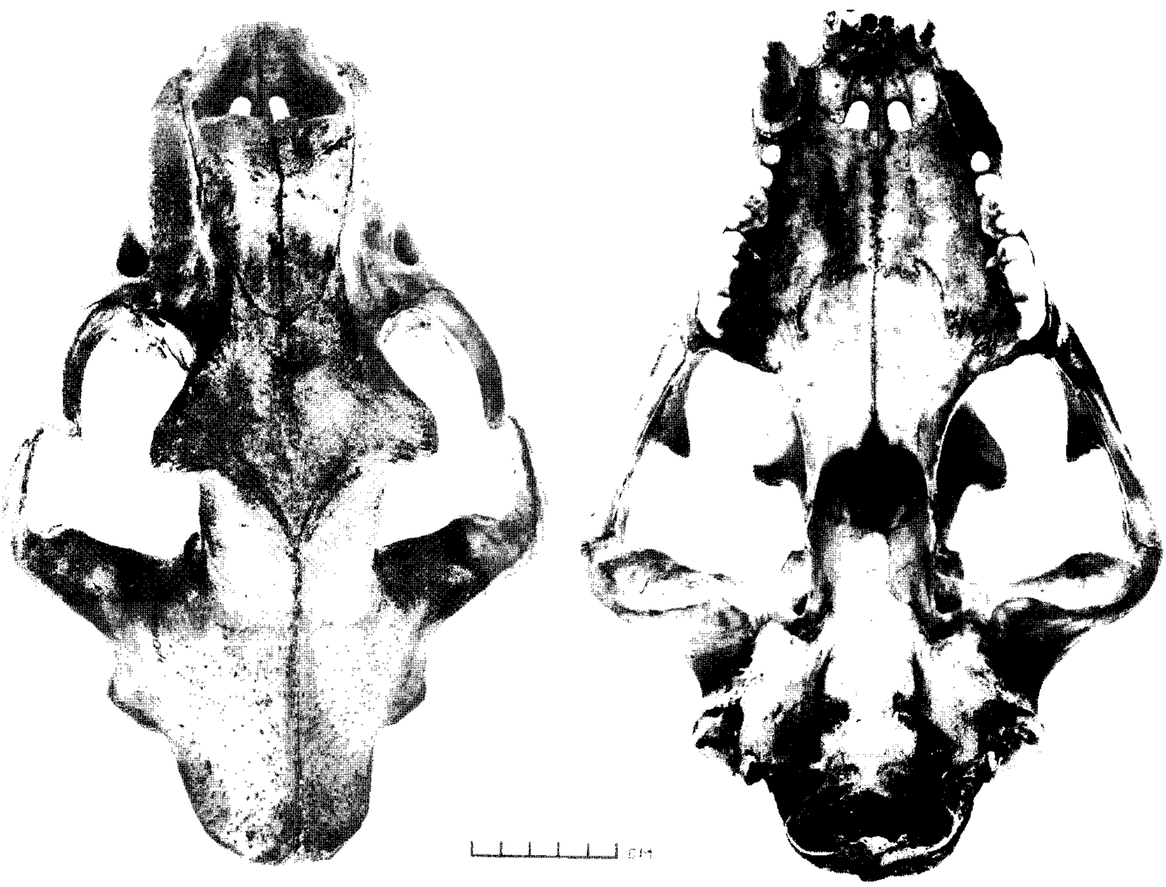

Fig. 5 Skull of *Panthera spelaea vereshchagini* n. subsp. from Duvanny Yar, Kolyma river (YGI 3190/1). Paratype. Palatal (right) and dorsal (left) views.

Schedel van *Panthera spelaea vereshchagini* n. subsp. (nieuwe ondersoort) van Duvanny Yar, Kolyma rivier (YGI 3190/1). Paratype. Onderaanzicht (rechts) en bovenaanzicht (links)

(1968), Vereshchagin (1971), Hemmer (1974), Harington (1977, 1996), Kurtén (1985), and others.

Skull and mandible measurements (in millimetrers; Tables 1 and 4, respectively) were taken according to standard techniques presented for *Felis* by Driesch (1976: figs. 17, 24), with some additions. Length and width of the canine were obtained in a measuring box; other measurements were made by calipers with an accuracy up to 0.1 mm. Craniometrical data was analyzed by means of the factor analysis program in STATISTICA for Windows.

Results

Sexual dimorphism

In European *Panthera spelaea*, males were larger than females, as in the recent lion (Turner, 1984). Sexual difference in skulls is expressed by the size of the canines. The length of the upper canine in *P. spelaea* from the North American part of Beringia ranges within limits of 25.7-29.4 mm for males and 18.7-21.2 mm for females (Kurtén, 1985). Accordingly, in our sample skulls from Duvanny Yar are males, while the skull from Mokhokho is most probably female.

Two analogous, presumably sexually dimorphic, size groups are also discerned in the sample mandibles on the bases of canine length and width. We refer to males mandibles with a canine greater than 26 mm in length and greater than 20 mm in width. Female mandibles possess canines with a length less than 25 mm and a width less than 19 mm. Gender assignment of the Yakutian mandibles can be further refined by mandibular length (distance between the central posterior face of the condyle process and the anterior face of the canine). The values of mandibular length in inferred males range within limits of 228 - 242 mm (n=4), which is in agreement with data on males of the fossil Beringian lion (Kurtén, 1985).

Skull

Extreme sexual dimorphism in skulls requires separate comparison of cranial measurements for male and female pleistocene lions. Measure-

Table 4 Size of mandibles (in mm) of middle pleistocene *Panthera spelaea vereshchagini* n. subsp. from Yakutia

Grootte van onderkaken in mm van *Panthera spelaea vereshchagini* n. subsp. (nieuwe ondersoort) van Yakutia, Midden Pleistocene

Measurements	Males		Females	
	Ulakhan Sullar, Adycha River	Beresovka River, Kolyma River	Beresovka River, Kolyma River	
	MM 6880	ZIN 31823	GIN 833-104	ZIN 29405
1	271.0	248.6		222.0
C_1-M_1 L	142.0	127.6	124.9	122.0
P_3-M_1 L	82.0	77.2	70.3	75.3
8	133.0	115.7	117.6	
9	54.9	54.0	51.3	49.2
10	51.0	51.1	46.2	44.7
Teeth:				
C_1 L	32.4	28.1		
C_1 W	22.0			
P_3 L	19.3			
P_3 W	11.1			
P_4 L	29.5	27.1		25.2
P_4 W	14.7	13.6		12.7
M_1 L	30.5	26.8	27.0	28.5
M_1 W	15.1	14.5	13.0	14.6

ments for both sexes of the Yakutian lion are given in table 1. These indicate the small size of individual animals relative to those in samples from other geographical regions (table 2).

The complete skull from Dawson Locality 10 (Yukon Territory, Canada), on the bases of basal length and mastoid breadth (130.3 mm; Harington, 1977), is closely similar to specimens in our Yakutian collection. The size of the Dawson skull is slightly larger than that of male skulls from Duvanny Yar, but the canine is narrower. The narrow canine suggests the Dawson skull is female. Two other fragmented but larger skulls from Dawson Locality 7 and 16 (Harington, 1977) are evidently males.

In southern central Siberia a neurocranium of a small lion (ZIN 32781) was found at Kurtak 4 on the Yenisei river, south of Krasnoyarsk. Its mastoid breadth, 124.2 mm, is very similar to the measurement of the female in our Yakutian sample.

Another small skull (edentulous; male; ZIN 32745) comes from Leninsk-Kuznetski in the southeastern portion of western Siberia. Its basal length (296.5 mm) and mastoid breadth (ca 134 mm) are similar to these variates in the Yakutia sample. However, the complete skull of a female (ZIN 32607) from the Altai Mountains is considerably larger (basal length = 290.1 mm; mastoid breadth = 138.2mm).

Male skulls of the late pleistocene cave lion *P. spelaea* (Goldfuss) from western Europe, the Caucasus and the Ural appreciably exceed the size of those of the fossil Beringian lion on the basis of average values for basal breadth, although in females the differences are less pronounced. Still larger was the American lion, *P. atrox* (Leidy), for example from the late pleistocene locality of Rancho La Brea, California, reported by Merriam and Stock (1932).

Thus, skull measurements indicate the presence of three allopatric, size-distinguishable, groups of lions in the Late Pleistocene of Holarctica: 1)

Table 5 Size of mandibles (in mm) of late pleistocene *Panthera spelaea vereshchagini* n. subsp. from Yakutia

Grootte van onderkaken in mm van *Panthera spelaea vereshchagini* n. subsp. van Yakutia, een nieuwe ondersoort uit het Laat Pleistoceen

Measurements	Males				Females	
	Ulakhan Sullar, Adycha River	Oner Lake, Ust-Aldan (Boeskorov & Lazarev, 1996)	Constantinovski Yar, Malyi Anui River	Bolshoy Lyakhovsky Island	Kyra Sullar, Adycha River	Ytyk-Kuel, Tata (Boeskorov & Lazarev, 1996)
	priv. coll.		GIN 836-295	GIN 367-247	MM 7315	
1	228.0	210.0	246.1	240.0	202.1	
C_1-M_1 L	120.7	118.0	124.9	119.4	105.6	112.0
P_3-M_1 L	72.3	77.0	75.1	75.5	62.8	67.8
8	95.3		117.6		101.3	
9	38.8		51.3	56.3	43.4	
10			46.2	55.2	38.5	
Teeth:						
C_1 L	29.0	26.4	29.5	ca 29.6	23.0	24.5
C_1 W	20.3	21.0	21.2	ca 21.0	18.9	14.7
P_3 L	20.1	19.0		21.2	15.6	16.4
P_3 W	10.0	8.6			7.5	8.8
P_4 L	25.9	27.0	28.6	28.0	23.3	25.3
P_4 W	14.5	12.0	12.7		10.8	12.5
M_1 L	29.0	27.0	29.2	26.6	23.9	27.2
M_1 W	13.0	14.0	14.6	13.4	10.4	13.2

Table 6 Geographical variability of length (in mm) of C1-M1 in pleistocene *Panthera spelaea* from the Holarctic

Geografische variatie in lengte (in mm) tussen de hoektand en de eerste kies in de onderkaak van de pleistocene *Panthera spelaea* van Holarctica.

Subspecies and localities:	n	lim	$\bar{x}$	N
Middle Pleistocene				
P. spelaea spelaea				
Aze I-3, France				
male (Argant, 1991	1	ca 149.4		
Kremenchug, Dnepr River				
male (Vereshchagin, 1971)	1	ca 130		
Shubnoe, Don River				
female (ZIN 29417)	1	122.7		
Manasurovo, Kama River				
female (Baryshnikov, 1992)	1	122.3		
Binagady, Transcaucasia				
female (ZIN 24409; Vereshchagin, 1971)	4	105.0-119.2	113.52	6.83
Total: males	2	130.0-149.4	139.70	
females	6	105.0-122.7	116.53	7.04
P. spelaea vereshchagini n. subsp.				
Yakutia (our data)				
males	2	127.6-142.0	134.80	
females	2	122.0-124.9	123.45	
Late Pleistocene				
P. spelaea spelaea				
Europe				
Jaurens, France				
male (Ballesio, 1980)	1	135.0		
Gailenreuth, Germany				
males (Dietrich, 1968; coll. NHM)	5	135.3-137.0	136.26	0.73
females (Dietrich, 1968)	1	131.0		
Wierzchowska Gorna, Poland (coll. ISEA)				
males	1	148.0		
females	5	108.0-128.0	120.22	8.23
Europe (Dietrich, 1968; Vereshchagin, 1971)				
males	1	131.0		
females	6	104.0-126.0	112.83	8.49
Urals (our data)				
males	2	140.0-163.0	151.50	
females	3	118.0-135.0	123.67	
Total: males	10	131.0-163.0	139.83	8.78
females	15	104.0-135.0	118.67	9.19
Western Siberia (coll. ZIN)				
males	3	134.5-138.5	136.00	2.18
females	1	119.2		
P. s. vereshchagini n. subsp.				
Yakutia (our data)				
males	4	118.0-124.9	120.75	2.98
females	2	105.6-112.0	108.80	
Chikoi River, Transbaikalia				
male (GIN 971/1889)	1	126.7		
Dawson, Yukon Territory (Harington, 1977)				
males	2	126.3-133.5	129.90	
females	1	116.7		
Total: males	7	118.0-133.5	124.21	5.34
females	3	105.6-116.7	111.43	5.57

animals of moderate size from western Europe, the Caucasus, the Ural, and possibly west Siberia, 2) animals of small size from Siberia and Beringia, and 3) animals of very large size in North America, south of the Wisconsinan Glaciation ice boundary.

To elucidate differences in cranial proportions among the samples, factor analyses were made for nine measurements. Data for both sexes were used in the analysis. The results are given in table 3 and figure 6. Based on a plot of the first two factors, the specimens fall into two groups, differentiated by Factor 2 (it includes measurements 17, 25 and 28). One of these groups comprised *P. spelaea* and the Beringian lion, the other group, *P. atrox*, which is characterized by a comparatively narrow auditory bulla and by weak compression of the postorbital constriction.

The last character is well shown on the scatter diagram plotting the breadth of the postorbital constriction and the mastoid breadth (fig. 7). The samples of *P. spelaea* and *P. atrox* only slightly overlap. In a scatter diagram, the specimens from the Asian and American portions of Beringia and from Siberia are found close to the European lion, and not close to the American lion. Thus, our data supports Kurtén's (1985) view that the fossil lion from Alaska and Yukon Territory is similar to *P. spelaea*. In this we differ with Harington (1977, 1996), who viewed the Yukon Territory lion to be *P. atrox* (his *Panthera leo atrox*).

It is both remarkable and unexpected that the complete skull of the large male lion from the late Middle Pleistocene of Aze I-3 in France (Argant, 1991), on the basis of factor analysis and regression of the breadth of the postorbital constriction

Table 7 Geographical variability of length (in mm) of the upper carnassial tooth, P4, in late pleistocene *Panthera spelaea* and *P. atrox* from the Holarctic

Geografische variatie in lengte (in mm) van de bovenkaaksknipkies, P4, in laat pleistocene *Panthera spelaea* en *P. atrox* van Holarctica

Subspecies and localities	n	lim	$\overline{x}$	N
P. spelaea spelaea				
Riss-Würm				
Tornewton, England (coll. NHM)	3	38.6-41.2	39.63	
Repolust, Austria (Schütt and Hemmer, 1978)	3	40.3-41.4	41.0	
Binagady, Transcaucasia (Vereshchagin, 1971)	2	34.4-35.0	34.70	
Würm/Wisconsinan				
Arrikrutz, Spain (Altuna, 1981)	1	43.0		
Jaurens, France (Ballesio, 1980)	4	35.0-36.8	35.85	0.98
Gerde, France (Clot, 1980)	3	38.0-38.9	38.50	
L'Herm, France (Clot, 1980)	7	40.3-42.0	41.3	
Bourgogne, France (Argant, 1991)	3	40.0-43.6	41.37	
Gailenreuth, Germany (coll. NHM)	4	36.6-41.2	39.0	1.88
Steiermark, Germany (Schütt and Hemmer, 1978)	4	(38)-40.3	39.2	
Germany (Schütt and Hemmer, 1978)	7	33.8-42.4	38.4	
Wierzchowska Gorna, Poland (coll. ISEA)	10	36.3-43.2	40.34	2.42
Europe (Vereshchagin, 1971; coll. ZIN)	12	35.0-40.4	37.77	1.28
Urals (Vereshchagin, 1971; our data)	4	36.5-38.0	37.50	0.71
Total	34	35.0-43.6	38.74	2.46
P. spelaea vereshchagini n. subsp.				
Yakutia (our data)	3	35.5-38.1	36.87	
Kurtak 4, Yenisei River (ZIN 32781)	2	37.4-37.8	37.60	
Dawson, Yukon Territory (Harington, 1977)	2	34.8-38.4	36.60	
Total	7	34.8-38.4	37.00	1.36
P. atrox				
Rancho la Brea, California (Merriam and Stock, 1932)	15	35.0-45.0	39.43	2.43

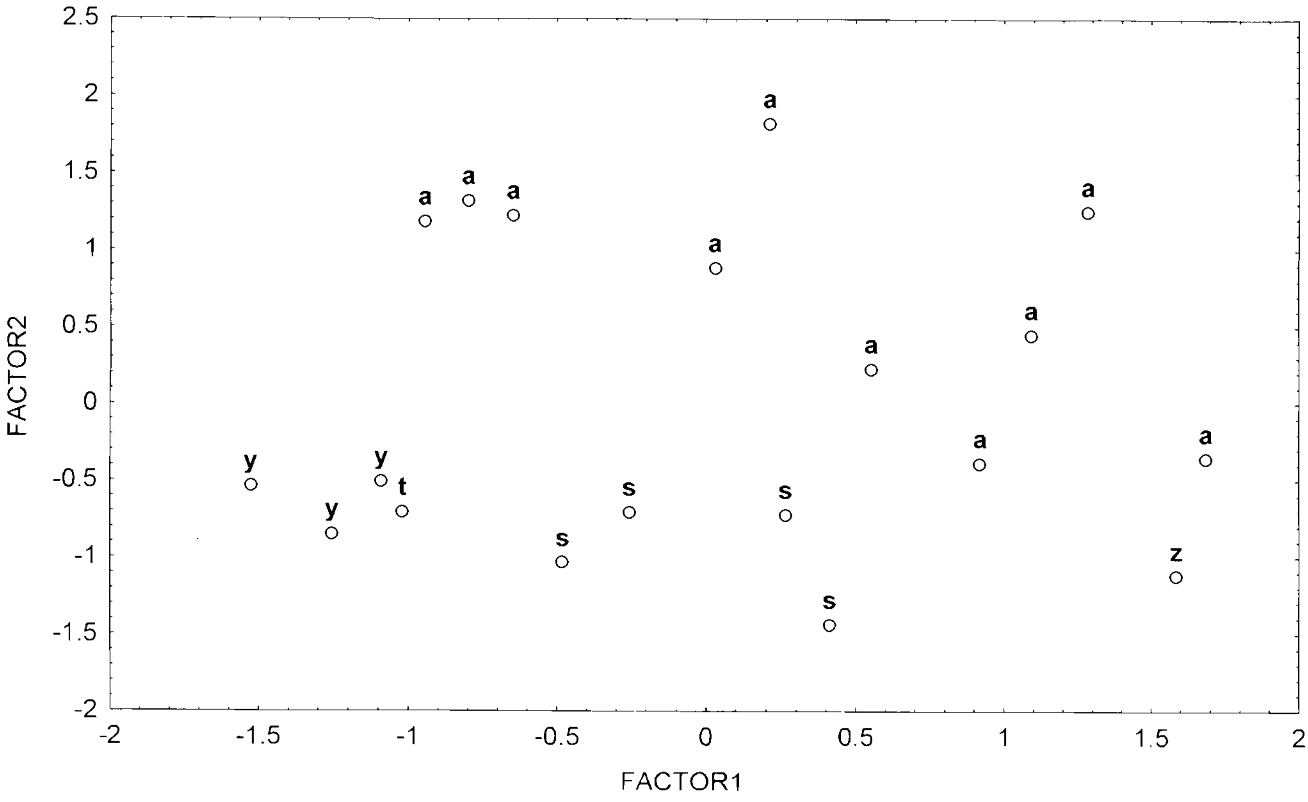

Fig. 6 Factor analysis based on 9 skull measurements in pleistocene *Panthera spelaea* and *P. atrox* from the Holarctic. a: *P. atrox* (Merriam & Stock, 1932), s: *P. spelaea* (Vereshchagin, 1971; our data), t: *P. s. vereshchagini* n. susbsp., Yukon Territory (Harington, 1977), y: *P. s. vereshchagini* n. subsp., Yakutia (our data), z: *P. spelaea*, Aze I-3 (Argant, 1991)

Factor analyse gebaseerd op 9 schedelmaten van pleistocene *Panthera spelaea* en *P. atrox* van Holarctica. a: *P. atrox* (maten uit Merriam & Stock, 1932), s: *P. spelaea* (maten uit Vereshchagin, 1971, aangevuld met eigen gegevens), t: *P. s. vereshchagini* n. susbsp., Yukon Territory (maten uit Harington, 1977), y: *P. s. vereshchagini* n. subsp., Yakutia (eigen gegevens), z: *P. spelaea*, Aze I-3 (maten uit Argant, 1991)

and mastoid breadth, falls nearer to the sample of *P. atrox* than to the sample of *P. spelaea* (fig. 6, 7).

According to Hemmer (1974), the weak compression of the postorbital constriction is associated with the relatively large volume of the neurocranial cavity of the American lion in comparisons with the European lion, which would indicate a higher level of cephalization in the American form. We infer therefore that the lions of the Old and New World may have had ethological differences. In this regard we are mindful of the opinion, arising from the equal occurrence of males and females of different age groups in the material from Rancho La Brea, that American lions, unlike European cave and modern African lions, were not gregarious and did not hunt in groups (Jefferson, 1992).

To summarize, on the basis of skull proportions the fossil lion from Yakutia is united with *P. spelaea*, as well as with the lions from Siberia and the Yukon Territory. The Yakutia lion differs from the cave lion only by smaller average values of recorded measurements. We attribute to the small fossil Beringian lion the samples from east Siberia (including Yakutia), Alaska, and the Yukon Territory. Average values of mastoid breadth in male (137.60 mm, n=5) and female (126.23 mm, n=3) (Harington, 1977; our data) Beringian lions are less than mastoid breadths in male (148.11 mm, n=7) and female (132.73 mm, n=6) cave lions (Vereshchagin, 1971; our data). However, these differences are statistically insignificant for both sexes.

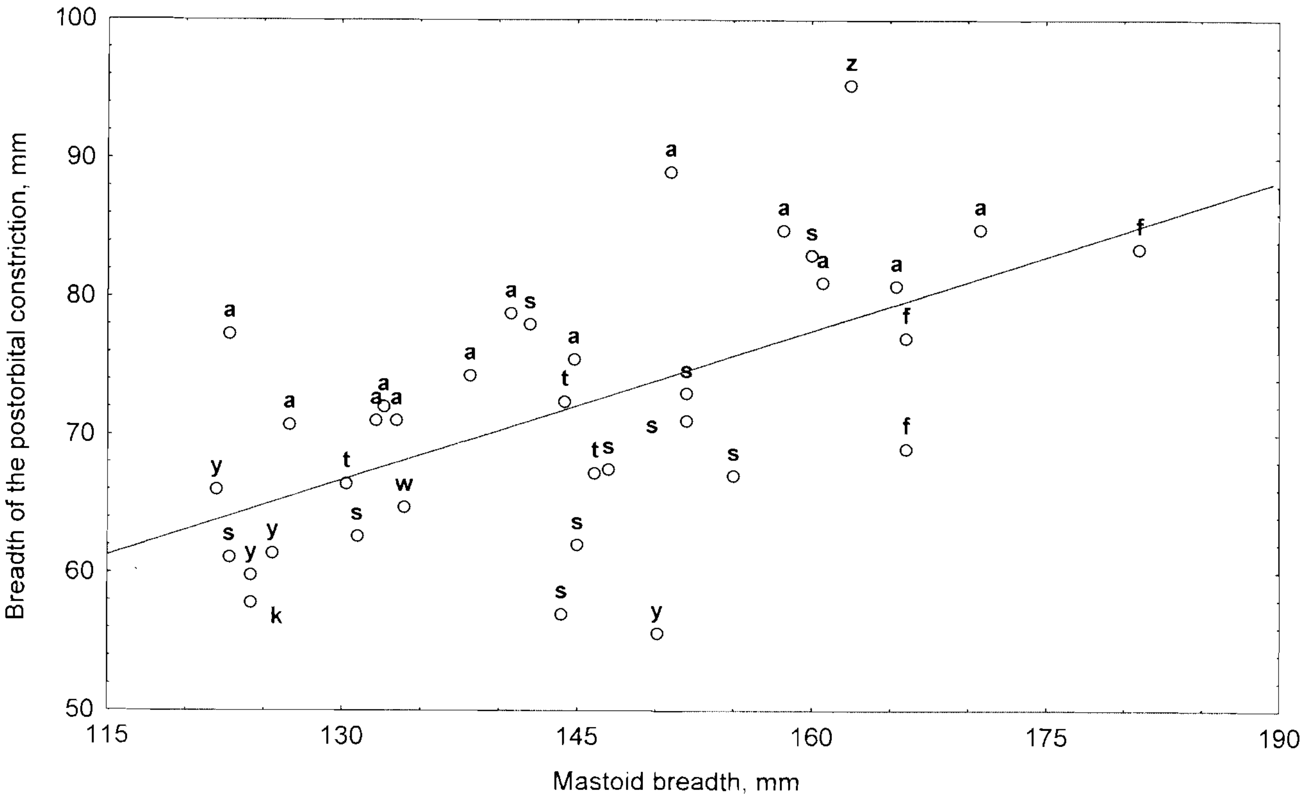

Fig. 7 The relationship between mastoid breadth and breadth of the postorbital constriction in pleistocene *Panthera spelaea* and *P. atrox* from the Holarctic. a: *P. atrox* (Merriam & Stock, 1932), f: *P. s. fossilis* (Kurtén & Poulianos, 1977; our data), k: *P. s. vereshchagini* n. subsp., Kurtak in Southeastern Siberia (our data), s: *P. s. spelaea*, Europe (Vereshchagin, 1971; Kurtén & Poulianos, 1977; our data), t: *P. s. vereshchagini* n. subsp., Yukon Territory (Harington, 1977), w: *P. s. spelaea*, western Siberia (our data), y: *P. s. vereshchagini* n. subsp., Yakutia (our data), z: *P. spelaea*, Aze I-3 (Argant, 1991)

Verhouding tussen de breedte van het mastoid en de breedte van de postorbitale vernauwing in pleistocene *Panthera spelaea* en *P. atrox* van Holarctica. a: *P. atrox* (maten uit Merriam & Stock, 1932), f: *P. s. fossilis* (maten uit Kurtén & Poulianos, 1977, aangevuld met eigen maten), k: *P. s. vereshchagini* n. subsp., Kurtak in Zuid-oost Siberie (eigen maten), s: *P. s. spelaea*, Europa (maten uit Vereshchagin (1971) en Kurtén & Poulianos (1977), aangevuld met eigen maten), t: *P. s. vereshchagini* n. subsp., Yukon Territory (maten uit Harington, 1977), w: *P. s. spelaea*, West Siberië (eigen maten), y: *P. s. vereshchagini* n. subsp., Yakutia (eigen maten), z: *P. spelaea*, Aze I-3 (maten uit Argant, 1991)

Mandible

Measurements of lower jaws of fossil lions from Yakutia are presented in Tables 4 and 5. Specimens from the Middle Pleistocene are shown to be larger than those from the Late Pleistocene, a difference observed both for males and females.

Mandibles from the Berezovka river are, on the basis of total length of the symphysis (83.6 and 72.8 mm) and size of cheek teeth, similar to lower jaws of *Panthera youngi* (Pei) from Locality 1 at Zhoukoudian (old spelling: Choukoutien), in China (Pei, 1934). The height and thickness of the horizontal ramus of the Zhoukoudian *Panthera*, however, are somewhat larger. In addition, in specimens from the Berezovka River, on the lingual side of M_1 at the point where the paraconid and protoconid contact, there is an enamel tubercle-like projection that is typical for *P. leo* and *P. spelaea* (Vereshchagin, 1971). On the basis of a drawing by Pei (1934: fig. 40, b) *P. youngi* lacks this projection.

Comparison of the length of the lower tooth row C_1-M_1 in lions from the late Middle Pleistocene of Europe and the Middle Pleistocene of Yakutia (table 6) do not show size differences between them. The mandible from Aze I-3 in France, however, on the basis of total length (285.4 mm)

Table 8 Geographical variability of length (in mm) of the lower carnassial, M1, in *Panthera spelaea* and *P. atrox* from the Holarctic, Pleistocene

Geografische variatie in lengte (in mm) van de onderkaaksknipkies, M1, in pleistocene *Panthera spelaea* en *P. atrox* van Holarctica

Subspecies and localities	n	lim	x̄	N
Middle Pleistocene				
P. spelaea fossilis				
Mauer and Mosbach, Germany (Schütt, 1969)	7	27.8-32.9	29.8	
Petralona, Greece (Kurtén and Poulianos, 1977)	1	31.0		
Cherny Yar, Volga River (Vereshchagin, 1971)	1	29.5		
P. spelaea spelaea				
Aze I-3, France (Argant, 1991)	1	31.3		
Kremenchug, Dnepr River (Vereshchagin, 1971)	1	31.4		
Shubnoe, Don River (ZIN 29417)	1	27.5		
Mansurovo, Kama River (Baryshnikov, 1992)	1	30.4		
Total	4	27.5-31.4	30.15	1.82
P. spelaea vereshchagini n. subsp.				
Yakutia (our data)	4	26.8-30.5	28.20	1.71
Late Pleistocene				
P. spelaea spelaea				
Riss-Würm				
Tornewton, England (coll. NHM)	11	25.7-30.8	28.38	1.77
Repolust, Austria (Schütt and Hemmer, 1978)	10	26.8-33.0	30.40	
Binagady, Transcaucasia (coll. ZIN)	2	29.0-29.1	29.05	
Würm/Wisconsinan				
Europe				
Jaurens, France (Ballesio, 1980)	7	27.0-30.0	28.30	1.24
L'Herm, France (Clot, 1980)	7	30.0-32.4	31.3	
Gailenreuth, Germany (Dietrich, 1968)	13	28.0-32.2	29.98	1.17
Germany (Schütt and Hemmer, 1978)	18	26.4-31.7	28.90	
Wierzchowska Gorna, Poland (coll. ISEA)	20	26.4-33.3	30.07	2.01
European Russia (Vereshchagin, 1971; coll. ZIN)	6	25.5-30.0	27.40	2.07
Urals (our data)	8	26.2-33.6	30.24	2.45
Total	42	25.5-33.6	29.43	2.19
Total, males only (Kurtén, 1985)	77	28.3-33.5	30.73	1.51
Western Siberia				
Krasny Yar, Ob River (ZIN 32746)	3	27.0-32.0	29.00	
P. spelaea vereshchagini n. subsp.				
Yakutia (our data)	6	23.9-29.2	27.15	1.92
Chikoi River, Transbaikalia (GIN 971/1889)	1	29.1		
Dawson, Yukon Territory (Harington, 1977)	1	27.5		
Sixtymile, Yukon Territory (Harington, 1977)	1	28.9		
Total	9	23.9-29.2	27.60	1.72
Total, males only (Kurtén, 1985)	15	27.0-33.2	28.81	1.56
P. atrox				
Rancho la Brea, California (Merriam and Stock, 1932)	17	26.9-33.9	29.51	2.10
Total, males only (Kurtén, 1985)	19	29.8-34.2	31.68	1.47

(Argant, 1991) exceeds the largest known specimen from Yakutia.

Clearer evidence of geographical variability in *P. spelaea* and *P. atrox* in the Holarctic are found in specimens dating to the last glaciation. Fossil Beringian lions from Yukon Territory (Harington,1977), on the basis of length of the C_1-M_1 tooth row, are very similar to those from Yakutia. A mandible from the Chikoi river in western Transbaikalia (GIN 971/1889) also has an analogous length. The specimens from Krasnyi Yar in the Ob river valley (ZIN 32746) and a specimen from Saltymakovo in the Tom river valley (ZIN 32747) in west Siberia are considerably larger. They correspond in total length of mandible and length of the tooth row to European *P. spelaea spelaea*. The last subspecies, on the basis of length of the C_1-M_1 tooth row, is remarkably larger than the fossil Beringian lion (table 6), having statistically significant differences in both males (t=4.54, P0.001) and females (t=1.81, P0.1).

In the American lion, *P. atrox*, sizes were somewhat larger as evidenced by average values for total length of mandibles in males: *P. atrox* - 288.23 mm (n=7), *P. spelaea fossilis* - 289 mm (n=1), *P. s. spelaea* from Europe - 262.98 mm (n=5), from western Siberia - 267.50 mm (n=3), from Beringia - 246.53 mm (n=7) (Merriam & Stock, 1932; Whitmore & Foster, 1967; Vereshchagin, 1971; Harington, 1977; Altuna, 1985; Argant, 1991; Groiss, 1992; our data). The fossil Beringian lion on this basis is significantly smaller than other studied samples (P0.1). The difference between mandibles of P. *spelaea* and *P. atrox* (P0.1) is also statistically significant on the basis of total length.

Thus, geographical variation in the size of mandible for the fossil lion from the Late Pleistocene of the Holarctic further corroborates the occurrence of three spatial groups, already noted from skull measurements. Due to the larger number of mandibles available for analysis, differences between the three groups were shown to be statistically significant in this case.

Dentition

Geographical variation in size of the fossil lions from the Holarctic may be observed by study of the upper and lower carnassial teeth, which were not divided on the basis of sex. The upper carnassial tooth, P^4, in the late pleistocene Beringian lion is on average shorter than in *P. s. spelaea* and *P. atrox* (Table 7). In each comparison, the differences are statistically significant (t=2.63, P0.001 and t=3.00 P0.01 respectively). However, *P. s. spelaea* and *P. atrox* are not significantly different on the basis of P^4 length (t=0.91).

The proportional length of the P^4 blade (relative to P^4 length) in the fossil lion from eastern Siberia (36.5- 37.7, mean 36.67%, n=3) is analogous to the length of the P^4 blade in *P. s. spelaea* (32.4-38.6, mean 36.23%, n=15). We therefore presume the diets of the Beringian lion and the European cave lion were similar.

The proportion indexes of length of P^4 : basal length of the skull in the Beringian lion (mean 13.07%, n=4) exceed those in *P. spelaea spelaea* (mean 12.04%, n=9) and *P. atrox* (mean 12.20%, n=15). The differences are statistically significant (0.01P0.1). Therefore, despite its small size, the fossil Beringian lion had a relatively large upper carnassial tooth.

The length of the lower carnassial tooth, M_1, in the fossil Beringian lion (Table 8) is significantly less than in *P. spelaea spelaea* (t=2.76, P0.01) and *P. atrox* (t=2.50, P0.01). This difference was especially marked for the M_1 of males, when these were considered separately (see Kurtén, 1985). Differences in the length of M_1 in *P. spelaea spelaea* and *P. atrox* proved to be insignificant (t=0.13), although according to Kurtén's (1985) data there is a significant difference between the males (t=2.50, P0.02) of the two forms.

Jefferson (1992) calculated body mass of *P. atrox* on the basis of M_1 size. Analogous calculations by us for fossil Beringian lion gave masses of 194 kg for males and 154 kg for females. Male Beringian lions were 21% larger than females, in contrast with *P. atrox* (males 31% larger) and with the recent African *P. leo* (males 15% larger) (Schaller, 1972; Jefferson, 1992). Differences in size relationships between the sexes in the different subspecies may be considered as an index of variety of social organization within the species. For example, the Beringian lion may have hunted in smaller prides than modern lions do, perhaps even in pairs or as single individuals as proposed by Guthrie (1990).

Discussion

Our results indicate that a unified geographical form of a small lion inhabited east Siberia, Alaska, and the Yukon Territory in the Late Pleistocene. This fossil Beringian lion was smaller than the nominative subspecies *P. spelaea spelaea* as well as *P. atrox*, and in skull proportions was nearer the former. This corroborates Kurtén's view (1985) that northwestern North America was inhabited by a taxon distinct from *P. atrox*. Kurtén (1985) pointed out only slight size differences between the fossil Beringian lion and the European cave lion and supposed that the former was a clinal variant of *P. spelaea*. Our data, however, shows that significant size differences exist on the basis of measurements of mandibles and teeth.

This small lion of the Late Pleistocene (Würm, Weichselian, and Wisconsinan Glaciations) was distributed throughout Beringia and elsewhere in east Siberia, for example in the west to the Yenisei river and in the south to western Transbaikalia. During the same interval, the larger cave lion (*P. spelaea spelaea*) inhabited western and eastern Europe, Transcaucasia, and the Ural Mountains. Discoveries of lions in west Siberia are still too rare to evaluate their systematic affinity, but available data allow us for now to group them more closely with the larger cave lion.

We can not confirm with certainty the gradual diminution in size of the fossil lion from west to east in Eurasia as being of a cline character. Most probably our data reveal the presence, in the Late Pleistocene of Eurasia, of two allopatrically distributed geographical races of *P. spelaea*. In our view the available data is quite sufficient to treat them as separate taxa of subspecific rank: *P.spelaea spelaea* and *P. spelaea vereshchagini* n. subsp.

Africa is the centre of origin of *P. leo*, where the species is known from the Early Pleistocene (Hemmer, 1974). *P. tigris* is known from the Middle Pleistocene in Asia. In western Europe, cats from the *leo-tigris* group were first recorded from numerous Cromerian localities (Schütt, 1969; Kurtén & Poulianos, 1977; Sala, 1990; Groiss, 1992). These Cromerian cats were referred to a very large subspecies of *P. spelaea*, *P. spelaea fossilis* (von Reichenau) (terra typica: Mosbach and Mauer, Germany). On the basis of basal length of skull (370-398 mm in males), *P. spelaea fossilis* was only slightly smaller than *P. atrox*. We also attribute to *P. spelaea fossilis* very large limb bones from middle pleistocene sites along the Volga and lower Tunguska river (Gromova, 1932; Vangengeim, 1961; Vereshchagin, 1971). These Russian remains testify to the occurrence of this subspecies eastward beyond the limits of western Europe.

The smaller (relative to *P. s. fossilis*) *P. spelaea spelaea* appeared in the late Middle Pleistocene of Europe. During its evolution its size did not change considerably, although there was some size increase during the last glaciation. Nor is remarkable size variation in time noted for the American lion, *P. atrox* (Kurtén & Anderson, 1980). In the history of the lion from eastern Siberia, however, a trend toward decreasing size can be traced.

The greatest length of the lion ulna from the lower Tunguska river (425 mm) appreciably exceeds the length of specimens available from Yakutia and Transbaikalia (346-365 mm, n=3), dated to a later time. Mandibles from the Berezovka river are also somewhat larger than specimens from the late pleistocene localities (see above). Size decrease is therefore a peculiarity of the Beringian lion during the second half of the Pleistocene.

Although data on the early evolution of the Beringian lion are fragmentary, we presume that the subspecies *P. spelaea vereshchagini* n. subsp. already began to differentiate in the Middle Pleistocene. Most probably the subspecies substituted for *P. spelaea fossilis* in eastern Siberia in the same manner as *P. spelaea spelaea* did as it appeared in Europe.

We consider the reason for the differentiation of the smaller-sized *P. spelaea vereshchagini* n. subsp. to have been the less favorable living conditions for lions in eastern Siberia and Beringia. These conditions presumably included low winter temperature extremes, a lengthy duration of snow cover, and an elusive or growth-limiting food base.

Numerous fossil remains of the Beringian lion, found both in different regions of continental Yakutia and on the Arctic islands (fig. 1), indicate that *P. spelaea* had been a quite usual element in the pleistocene fauna of arctic Siberia. At the same time, severe climatic conditions demanded of this species the creation of an economical form expending less energy to maintain vital functions. Thus came to be, especially, a decrease in body size allowing these predators to rapidly satisfy their hunger and thus maximize their foraging efforts.

Diminution of size in the late Pleistocene occurred in many large mammals in Yakutia, for example in the brown bear (Baryshnikov & Boeskorov, 1998) as well as in bison and other herbivores (Russanov, 1975). Well-known examples of diminution in size of larger cats under conditions of insular isolation are also primarily due to limitations in the food supply. This was presumably the case for the now extinct dwarf tiger, *P. tigris balica* (Schwarz) from Bali, Indonesia.

Systematics

Order Carnivora Bowdich, 1821
Family Felidae Fischer, 1817
Genus *Panthera* Oken, 1816
Panthera spelaea (Goldfuss, 1810)
Terra typica. Gailenreuth Cave, Germany, Late Pleistocene.
Panthera leo vereshchagini Baryshnikov et Boeskorov n. subsp.

Etymology. Named in honour of the Russian zoologist, Professor Nikolai K. Vereshchagin.
Holotype. Female skull without mandible, coll. ZIN 29398; Mokhokho, Olenek river in Yakutia, Late Pleistocene, collected by Ph. Iliin, 1963.
Paratypes. Two male skulls without mandibles, coll. YIG 6397 and 3190/1; Duvanny Yar, Kolyma river in Yakutia, Late Pleistocene.
Diagnosis. The smallest subspecies of the pleistocene lion-like cat from the northern part of the Holarctic. Differing from *P. spelaea spelaea* by smaller mean size, and from *P. atrox* by smaller mean size and by the relatively narrow postorbital constriction.
Size (for the Late Pleistocene form). Length of the upper tooth row C^1-P^4: 102-103 mm for males (n=2) and 98-99 mm for females (n=2); length of the lower tooth row C_1-M_1: 118-133.5 mm (mean 124.2 mm, n=7) for males, 105-117 mm (mean 111.4 mm, n=3) for females.
Distribution: Late and possibly the late Middle Pleistocene in eastern Siberia and Beringia, including Alaska and Yukon Territory.

Note: Freudenberg (1914) has been among the first scientists who pointed out that fossil remains of the large cat found in Siberia belonged to the lion, and not to the tiger. This researcher thought that the fossil Siberian lion also penetrated Europe and he described it as *Felis spelaea* var. *sibirica*. However, according to Hemmer (1974: 263), this name is based on material from Steeden in Germany, and consequently could not represent the lion from eastern Siberia. It is rather a junior synonym of *P. spelaea spelaea*.

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Addresses of the authors

Gennady Baryshnikov
Zoological Institute
Russian Academy of Sciences
199034 St. Petersburg
Russia
e-mail:BGF@zisp.spb.su

Gennady Boeskorov
Mammoth Museum
Yakutian Academy of Sciences
677891 Yakutsk
Russia

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