

## The Pleistocene lion of Beringia

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The late Pleistocene lion of Beringia was a distinctly smaller animal than the great *Panthera leo atrox* south of the Wisconsin ice. It probably was on a cline with the slightly larger European *Panthera leo spelaea* and is referred to the same taxon.

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### 1. Introduction

Beringia is the name given to the sub-continent connecting Siberia with Alaska during Pleistocene glacial-eustatic regressions (see Hopkins 1967). Bounded to the west by the Kolyma River, and to the east by the North American inland ice, it comprised easternmost Siberia with Kamchatka Peninsula as an outlier, parts of Alaska, the Yukon, and the Northwest Territories, as well as a large expanse of the now-submerged Bering-Chukchi Platform. Pleistocene deposits in Alaska and the Yukon have produced a rich mammalian fauna (see Kurtén & Anderson 1980:40-44, 88-89).

The presence of a lion-like cat in Alaska was reported by Frick (1930) and numerous finds are now on record from Alaska and the Yukon (see Harington 1969). The Pleistocene lion of North America was described under the name *Felis atrox* by Leidy in 1853 (*F. imperialis* Leidy, 1873 is a synonym). However, Hemmer (1974) and others regard it as a subspecies (*Panthera leo atrox*) of lion and I concur with this opinion. In the late Pleistocene this taxon was widespread in North America south of the Wisconsin ice, except in the east and in peninsular Florida, and ranged into South America (see Kurtén & Anderson 1980:191-192). The Beringian cat has mostly been referred to *P. l. atrox* (Harington 1969), but Vereshchagin (1971) considered the Beringian lion to represent the Eurasian *P. l. spelaea* rather than *atrox*.

In the present study, metric characters of the Beringian lion are compared with those for *P. l. atrox* and *P. l. spelaea*. The results support

Vereshchagin's conclusion of a closer relationship with the Eurasian population.

### 2. Material

Beringian lion (Alaska and the Yukon)

The main part of the material comes from the Fairbanks region, Alaska, and is in the Frick Collection of the American Museum of Natural History, New York. Additional specimens were seen in the Smithsonian Institution, Washington, D.C., and in the National Museum of Natural Sciences, Ottawa, Canada. The age is Rancholabrean, probably mainly Wisconsinan.

*Panthera leo atrox* (U.S.A. and Mexico)

The sample includes material from California, Florida, Idaho, Nebraska, Nevada, Texas, and Mexico, and was studied in various museums; in addition, data published by Merriam and Stock (1932) were used. The largest local sample is that from Rancho La Brea, California, which makes up more than half of the total material. I have tested for differences between the Rancho La Brea lion and the remaining material. Such differences as occur are non-significant and random. The age is Rancholabrean, mainly Wisconsinan.

*Panthera leo spelaea* (Europe)

Material from Austria, Belgium, the Federal Republic of Germany, France, the German Democratic Republic, Great Britain, Poland, Spain, and Switzerland was studied in various museums; some data culled from the literature have been included. The age is Eemian and Weichselian; older material has been excluded.

*Panthera leo leo* (Africa)

Material in various European museums; also a sample in the Transvaal Museum, Pretoria, South Africa, kindly contributed by Dr. Alan Turner. The age is Recent.

### 3. Sexual dimorphism

A pronounced sexual dimorphism in size is a characteristic of large felines in general, and the lion is no exception. The idea that the two size groups (e.g. in the European cave lion) represent two distinct taxa has been voiced repeatedly, even quite recently (Ballesio 1975) but is certainly false (Turner 1984). Size distributions and the degree of dimorphism are very similar in fossil and Recent lion samples. However, the relative abundance of the two sexes may differ greatly at different sites, in part due perhaps to chances of preservation and sampling, but also to ethological factors as discussed by Turner. In the material available to me, males generally outnumber females, but ratios vary between localities. Thus, grand means for samples combining both sexes are apt to be misleading. All comparisons should be made between samples of the same sex.

Fortunately, the dimorphism is sufficiently great that nearly all well-preserved adult specimens in a sample (comprising both sexes) may be sexed. An analogous study of Recent puma, *Felis concolor* L. (Kurtén 1973), showed that the fraction of non-sexable specimens is negligible, if a combination of dental and cranial measurements is used. Variates which were found to be especially useful in sexing include size of canine teeth, carnassials, and mandible. The present exposition is based on these characters; however, it should be noted that all the pertinent variates were studied.

### 4. Comparison of samples

#### 4.1. Size of upper canines

The length and width of upper canine teeth in *P. l. atrox* and in Beringian lions are plotted in Fig. 1. As in corresponding plots for the Recent lions and the Pleistocene European cave lions (see Turner 1984), both samples show a division into two distinct size groups, evidently representing males and females. Table 1 gives the statistics, with corresponding data for the European *P. l. spelaea*.

Female canines are, on average, some 20 per cent smaller than male canines (when the male mean is set at 100%); the observed variation (18–23%) is unimportant. The intrasexual variation (measured by  $V$ , the coefficient of variation) is of the magnitude normally found in

Table 1. *Panthera leo*, measurements of upper canine teeth. — A = *P. l. atrox*, B = Beringian *P. leo*, S = *P. l. spelaea*. In this and subsequent tables,  $N$  is number of specimens,  $SE$  standard error,  $SD$  standard deviation, and  $V$  Pearsonian coefficient of variation.

		$N$	Range	Mean $\pm SE$	$SD$	$V$
Length	$\sigma \sigma$	A 15	29.0–36.8	31.54 $\pm$ 0.61	2.38	7.6
		B 10	25.7–29.4	27.49 $\pm$ 0.41	1.29	4.7
		S 20	25.4–32.7	29.42 $\pm$ 0.35	1.57	5.3
	$\varphi \varphi$	A 7	23.0–25.6	25.10 $\pm$ 0.36	0.94	3.8
		B 4	18.5–23.5	21.23 $\pm$ 1.04	–	–
		S 17	20.6–26.3	23.31 $\pm$ 0.34	1.41	6.1
Width	$\sigma \sigma$	A 15	20.4–25.7	22.71 $\pm$ 0.40	1.55	6.8
		B 11	18.7–21.2	19.75 $\pm$ 0.23	0.77	3.9
		S 24	18.5–24.8	21.35 $\pm$ 0.27	1.31	6.1
	$\varphi \varphi$	A 7	18.0–19.7	18.53 $\pm$ 0.21	0.55	3.0
		B 4	14.2–17.0	15.60 $\pm$ 0.57	–	–
		S 16	15.6–19.6	17.16 $\pm$ 0.29	1.16	6.8

Table 2. *Panthera leo*, males only, length of lower carnassial ( $M_1$ ). — R = Recent, Africa; other samples as in Table 1.

		$N$	Range	Mean $\pm SE$	$SD$	$V$
$\sigma \sigma$	A	19	29.8–34.2	31.68 $\pm$ 0.34	1.47	4.7
	B	15	27.0–33.2	28.81 $\pm$ 0.40	1.56	5.4
	S	77	28.3–33.5	30.73 $\pm$ 0.17	1.51	4.9
	R	15	28.0–30.8	29.23 $\pm$ 0.26	1.00	3.4

dental variates of homogeneous populations. (The sample of female Beringian canines is too small to give meaningful information on this parameter.)

In the male canines, the means for the three samples differ significantly in all cases. As regards the female means, the Beringian values are significantly lower than those for *P. l. atrox*, but the material is too small to establish significance in the comparison with *P. l. spelaea*. Nevertheless, the results are clear: the three samples represent a series of increasing size with the Beringian lion as the smallest, and *P. l. atrox* as the largest.

#### 4.2. Size of lower carnassials

The size relationships of the cheek teeth are similar to those of the canines. As an example, statistics for the lower carnassial ( $M_1$ ) in male lions are recorded to Table 2. I have included

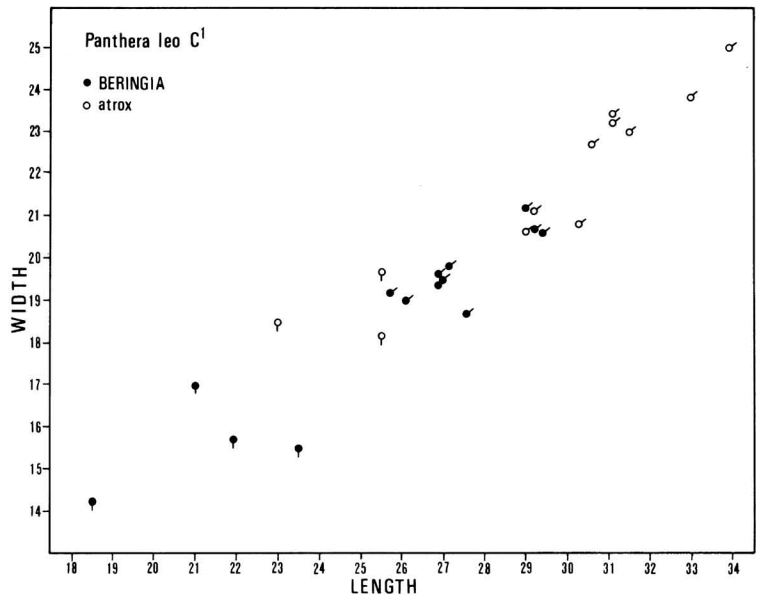


Fig. 1. Width and length of upper canine tooth in fossil lion from Beringia and in *Panthera leo atrox*, as labelled. Material sexed according to size. See text for data and discussion.

data for Recent African lions. It may be noted that the Beringian mean (although lower) does not differ significantly from the Recent. All other intersample comparisons indicate significant differences. Again, the Beringian lion is the smallest, *P. l. atrox* the largest.

#### 4.3. Size of mandibles

Although tooth size is correlated with head size infraspecifically, the correlation is only moderately strong (see Kurtén 1967). The best available measure of relative head size (and of body size, since head and body size are closely intercorrelated) in the present material is the length of the mandible (here measured from the anterior face of the canine to the central posterior face of the condyle).

Distributions for this variate are shown in Fig. 2. The material has been sexed, mainly according to dental measurements. The Beringian sample shows bimodality and full dichotomy. The two other samples are probably also bimodal but there is some overlap, most likely due to inclusion of young adults which were not fully grown. It is believed that the inclusion of a large number of young males, plus the fact that only four female mandibles yielded this variate, produced the apparent unimodality in the *P. l. spelaea* sample. For the statistics see Table 3.

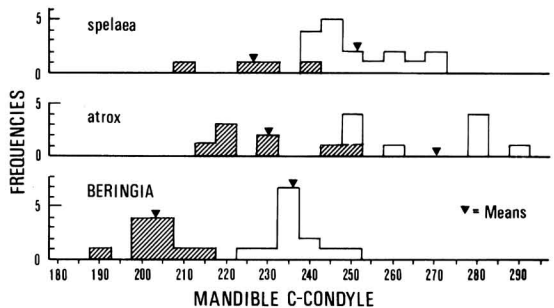


Fig. 2. Mandibular length in *Panthera leo spelaea* (Europe), *P. l. atrox* (North America), and fossil Beringian lion. The material has been sexed on the basis of mandibular and/or dental size: cross-hatched, females; white, males. Although clearly immature specimens have been excluded, a number of small *spelaea* and *atrox* males were probably not fully grown. Means for females and males are indicated.

Table 3. *Panthera leo*, mandibular length, anterior face of canine tooth to posterior face of condyle. Samples as in Table 1.

		N	Range	Mean $\pm$ SE	SD	V
♂ ♂	A	9	249-290	269.6 $\pm$ 5.5	16.4	6.1
	B	13	226-248	236.7 $\pm$ 1.6	5.9	2.5
	S	16	240-270	251.5 $\pm$ 2.5	10.1	4.0
♀ ♀	A	8	217-252	229.8 $\pm$ 4.6	12.9	5.6
	B	11	194-215	203.6 $\pm$ 1.7	5.7	2.8
	S	4	212-239	226.2 $\pm$ 5.6	-	-

The sexual dimorphism tends to be slightly greater in this variate (up to 25 %) than in the canines. The Beringian mandibles, male as well as female are, on average, significantly smaller than those of *P. l. atrox* and *P. l. spelaea*. Again, male *P. l. spelaea* are, on average, significantly smaller than male *P. l. atrox*. The females differ in the same way but the material is too small for significant results.

#### 4.4. Comparison with Siberian lion

There are records of lion in the late Pleistocene throughout Siberia from the European U.S.S.R. in the west to the Kolyma River basin in the east (Vereshchagin 1971); 27 sites were known in 1971. However, the number of specimens is smaller than that from Europe and from eastern Beringia. Vereshchagin records measurements of six mandibles, for which the salient data are reproduced here (Table 4). Four of the mandibles are from the Ob area, far to the west; the remaining two, from Bolshoi Island and the Kolyma, are from the western approaches to Beringia, and are of special interest in the present context.

Both are probably male. Mandibular and carnassial lengths agree well with data from Beringian male lion. Both mandibles are shorter than *P. l. atrox* males (lower limit 249) and the smaller one is shorter than European *P. l. spelaea* males (lower limit 240), although it is evidently adult (Vereshchagin 1971, plate 7, fig. 2). Carnassial lengths are within the observed range for both the Beringian lion and the European *P. l. spelaea* but bracket the lower limit for *P. l. atrox*. Thus, the lions of eastern Siberia compare with those of eastern Beringia, but are certainly smaller than *P. l. atrox*, and probably smaller than European *P. l. spelaea*.

Table 4. *Panthera leo*, Siberia, measurements of mandibles and carnassials (data from Vereshchagin 1971).

	Mandible length	M <sub>1</sub> length	M <sub>1</sub> width
Kolyma, Beresovka	226	30	14
Bolshoi Island	240	29	-
Ob, No. 2995	-	27	14
Ob, No. 2964	-	26	13
Ob, No. 2973	-	25	14
Ob, No. 64	-	23.7	13.2

#### 4.5. Conclusions

1. There is a strong discontinuity between Beringian lions and *Panthera l. atrox* south of the ice, the latter being a considerably larger form. This suggests that the Beringian lions should be regarded as belonging to a taxon distinct from *P. l. atrox*.

2. Beringian lions are somewhat smaller on average than European *P. l. spelaea*. The same appears to be true for the lions of eastern Siberia. The difference, however, is relatively slight, and the probability is that the Beringian lions were on a cline with the European ones. I conclude therefore that they are most properly referred to the subspecies *P. l. spelaea*.

#### 5. Discussion

The fact that the Wisconsinan large-mammal fauna of Beringia has a pronounced Palaearctic stamp has become increasingly evident in recent years. Beringia then comprised the eastern flank of the mammoth steppe (Guthrie 1982). Typical Palaearctic elements include *Equus hemionus*, *Cervalces latifrons*, *Saiga tatarica*, *Praeovibos priscus*, *Bison priscus*, *Bos grunniens*, and we might add *Mustela eversmanni*, none of which spread south of the ice or, if they did, they gave rise to distinct daughter species (*Cervalces scotti*, *Bison latifrons*, *Mustela nigripes*). Furthermore, *Ursus arctos* (and probably *Homo sapiens*) was confined to Beringia for most of the Wisconsinan, and migrated south at a late date. The Eurasian cave lion is thus another example of a typically Palaearctic taxon in the fauna of eastern Beringia.

Of course, that fauna also contained a number of species which had originated in the Nearctic (e.g. *Megalonyx jeffersonii*, *Arctodus simus*, *Mammot americanum*); they have so far only been recorded in eastern Beringia.

As noted above, several Palaearctic-Beringian species gave rise to distinct Nearctic species south of the ice. In other instances, the differentiation is subspecific at most (e.g. *Cervus elaphus*, *Alces alces*, *Ursus arctos*, and the extinct Amerian *Cuon alpinus*). The time of their introduction (Sangamonian to late Wisconsinan) tends to be more recent than in the instances of full specific differentiation. The lion evidently entered the Nearctic south of the ice in Sangamonian times (Kurtén &

Anderson 1980:191), which may also be true for *Cervus elaphus* and *Cuon alpinus*. In the case of the lion, the divergence between the forms north and south of the ice probably occurred very soon after its entrance in the area south of the ice, where it rapidly adjusted to the new conditions. For instance, there is good evidence (held by R. D. Guthrie) that the Beringian lion preyed on *Bison priscus*; south of the ice it would encounter the larger *B. latifrons*.

Whether other characters besides size were affected (for instance in the proportions of the postcranial skeleton) remains to be determined. The size difference alone is hardly sufficient to validate *P. atrox* as a distinct species.

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