

Systematic position of the cave lion *Panthera spelaea* (Goldfuss) based on cranial and dental characters

Marina Sotnikova*, Pavel Nikolskiy

Geological Institute, Academy of Sciences of Russia, Pyzhevsky line 7, 119017, Moscow, Russia

Available online 19 July 2005

Abstract

Well-preserved skulls of Late Pleistocene *Panthera spelaea* are described from two geographically distant regions of Russia situated in the Russian Plain and Northern Siberia. The resemblance of the studied material with contemporaneous fossil lions from Alaska is established. The cranial morphology of *P. spelaea* confirms its phylogenetic position within the lion group, whereas many of the characters supporting the cave lion's relationship with the tiger are primitive. Both living and cave lions are advanced relative to the Middle Pleistocene *P. fossilis* in having larger upper incisors and more inflated bullae. *P. spelaea* also possesses the following advanced characters in common with the living lion: widened muzzle in the canine and P2 areas, wide nasal bones, relatively short pre-orbital part of the skull, laterally widened mastoid area, V-shaped form of the posterior tip of the frontal process of maxillary bone, and reduced cusp on the protocone bulge of P4. These conditions establish *P. spelaea* as a distinct species.

© 2005 Elsevier Ltd and INQUA. All rights reserved.

1. Introduction

The great fossil lion of the Holarctic Late Pleistocene has been considered in the extensive literature under a variety of names: *Panthera spelaea* (Goldfuss) or *P. leo spelaea* for Eurasian samples and *P. atrox* (Leidy), *P. leo atrox* or *P. leo spelaea* for North American specimens.

We are compelled to reconsider this subject. First, during recent years there has been a prevalent tendency to regard the Eurasian cave lion as a subspecies of the living lion. Second, Baryshnikov and Boeskorov (2001) have re-opened the discussion on the separate subspecific status for the Beringian Late Pleistocene fossil lion. And third, the close relationship of *P. spelaea* to *P. tigris*

(L.) was recently restated on the basis of an analysis of their brain morphology (Groiss, 1996).

This paper reports new cranial specimens of cave lions from northeastern Siberia and from the Russian Plain, compares the geographically distant European and Asian samples with the population of fossil lions from northwestern North America, and finally considers their affinities and relationships on the basis of cranial morphology.

2. Materials and methods

Our study is based on new material of *P. spelaea* from Upper Pleistocene deposits of two geographically distant regions situated in the Russian Plain and Northern Siberia. Cranial remains have been recently excavated from the Russian Plain in the Upper Palaeolithic site of Avdeevo, Kursk Region, and in the Smolensk Region. In Northern Siberia, new finds of *P. spelaea* have originated from the Duvanniy Yar section and from the bank of Kondakovka Creek; both sites named are in the Kolyma River Basin in Eastern Siberia (Fig. 1).

Abbreviations: IPBPS—Institute of Physicochemical and Biological Problems in Soil Science, Russian Academy of Science, Pushchino, Moscow Region; ZMSU—Zoological Museum of Moscow State University; YIG—Yakutian Institute of Geology, Yakutsk; F: AM—the Frick collection of American Museum of Natural History; GIN—Geological Institute, Russian Academy of Science, Moscow; ZIN—Zoological Institute, Russian Academy of Science, St. Petersburg.

*Corresponding author.

E-mail addresses: sotnik@ginras.ru (M. Sotnikova), nikol@ginras.ru (P. Nikolskiy).

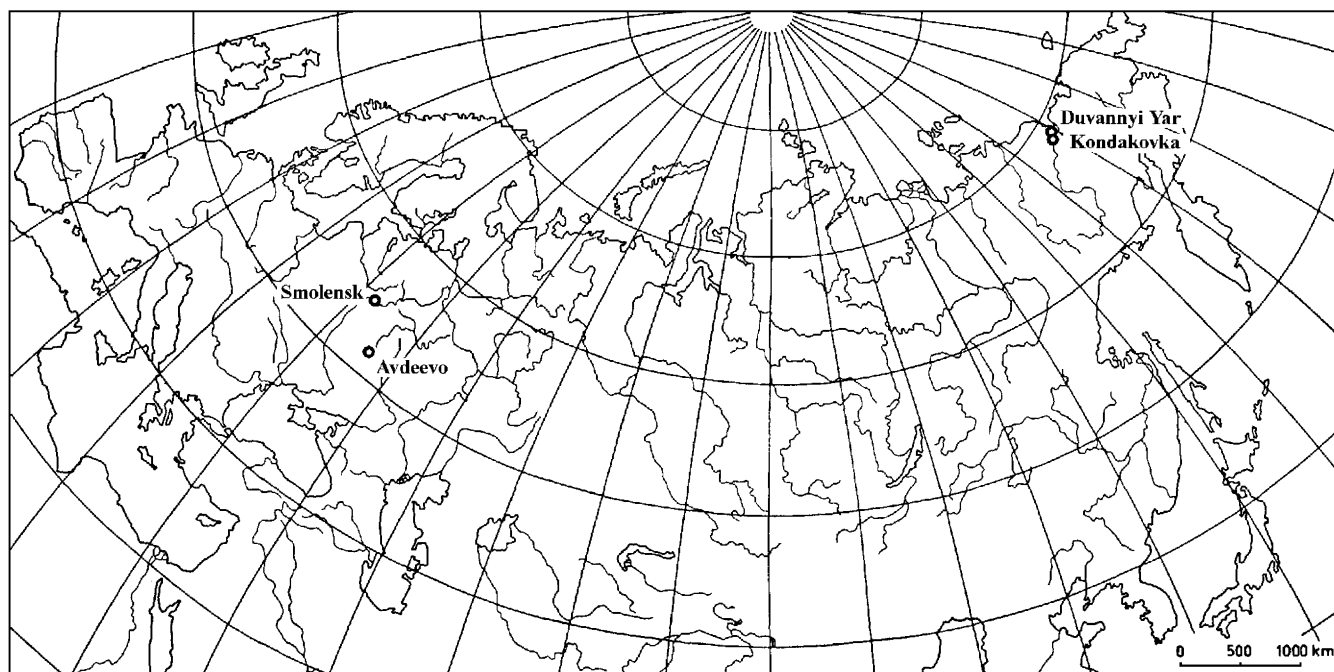


Fig. 1. Russian localities with cranial material of *Panthera spelaea* described in the text.

Duvanniy Yar is known as a rich mammalian faunal site associated with the yedoma-type sediments. The studied skull (IPBPS-1) was found at a height of 28m above the level of the Kolyma River (Gubin, pers. commun., 2003). Apart from our study of cranial material, two other skulls of cave lion, YGI 3190/1 and YGI-6397, have been described by Baryshnikov and Boeskorov (2001) from the Duvanniy Yar section. Both were also obtained from yedoma-type sediments, which are correlated with the second part of the Late Pleistocene. The skull YGI-6397 has been radiocarbon dated to 36.000 yr B. P. (GIN-8327).

Our reported materials are best represented by the nearly complete skulls belonging to three adult individuals from the Smolensk, Kondakovka and Duvanniy Yar localities. There are also partial cranial remains and upper teeth from the Avdeevo site.

A comparative analysis of a mixed sample of the skulls of lion-like cats, including both males and females, gives misleading results because of the high level of sexual dimorphism in these felines (Kurtén, 1985). Turner (1984, p. 4, Fig. 3) demonstrated a difference in the size of the upper canine between samples of male and female lions. Our cranial material was sexed according to canine size. All the skulls studied exhibited clearly pronounced male characteristics. Therefore, for comparative analysis we used only adult male skulls from recent and fossil animals.

Some previous workers suggested possible relationships between the Late Pleistocene great cat and *P.*

tigris, but most have placed the extinct lions such as *P. spelaea*, *P. atrox* and *P. fossilis* (Reichenau), within the lion lineage. The new material is closely compared with the above-mentioned taxa. Comparisons were made with skulls of the Late Pleistocene Alaskan fossil lions from the Frick Collection of the American Museum of Natural History: F:AM 30460, 69048, and 30751. Comparative material of living *P. leo* (L.) and *P. tigris* was studied in the collections of the Zoological Museum of the Moscow State University and in the Geological and Paleontological Institutions of Russian Academy of Science. Additional morphological and dimensional cranial information on Late and Middle Pleistocene lions were obtained from the literature (Merriam and Stock, 1932; Terzea, 1965; Dietrich, 1968; Harington, 1969; Vereshchagin, 1971; Wiszniowska, 1978; Argant, 1980, 1988, 1991; Altuna, 1981; Baryshnikov and Boeskorov, 2001).

The evaluation of principal cranial features and interpretation of their primitive or derived characters was partially based on a determined for carnivores by Flynn and Galiano (1982), Wyss and Flynn (1993) and especially for felids by de Beaumont (1964), Van Valkenburgh et al. (1990) and Martin (1997). For other comparison in some cases we referred to the cranial characters of the *Pseudaehurus* and to dolichocephalic members of the *Therailurus* Piveteau—*Dinofelis* Zdansky group of felids.

G.G. Simpson's (1941) method of ratio diagrams was used for the comparative dimensional cranial analysis. All measurements are in millimeter.

3. Systematic description

Order Carnivora Bowdich, 1821

Family Felidae Fisher, 1817

Genus *Panthera* Oken, 1816

Panthera spelaea (Goldfuss, 1810)

Referred specimens: GIN-1123, Smolensk area, a complete skull with partly damaged teeth and missing bilateral I1-2, P2, left P4 and M1, (Fig. 2A,B). IPBPS-1,

Duvannyi Yar locality, Kolyma River Basin, a nearly complete skull with partly broken zygomatic arches, palate, nasal, and basioccipital regions, left canine, bilateral I1-2, P2, M1, and right P4 are missing, other teeth are damaged (Fig. 2C,D). K-1 (private collection), bank of Kondakovka Creek, Kolyma River Basin, complete skull with partly broken nasal bones (Fig. 3A–D). GIN/AV86-12, Avdeevo locality, Kursk region, right P4 (Fig. 3E).

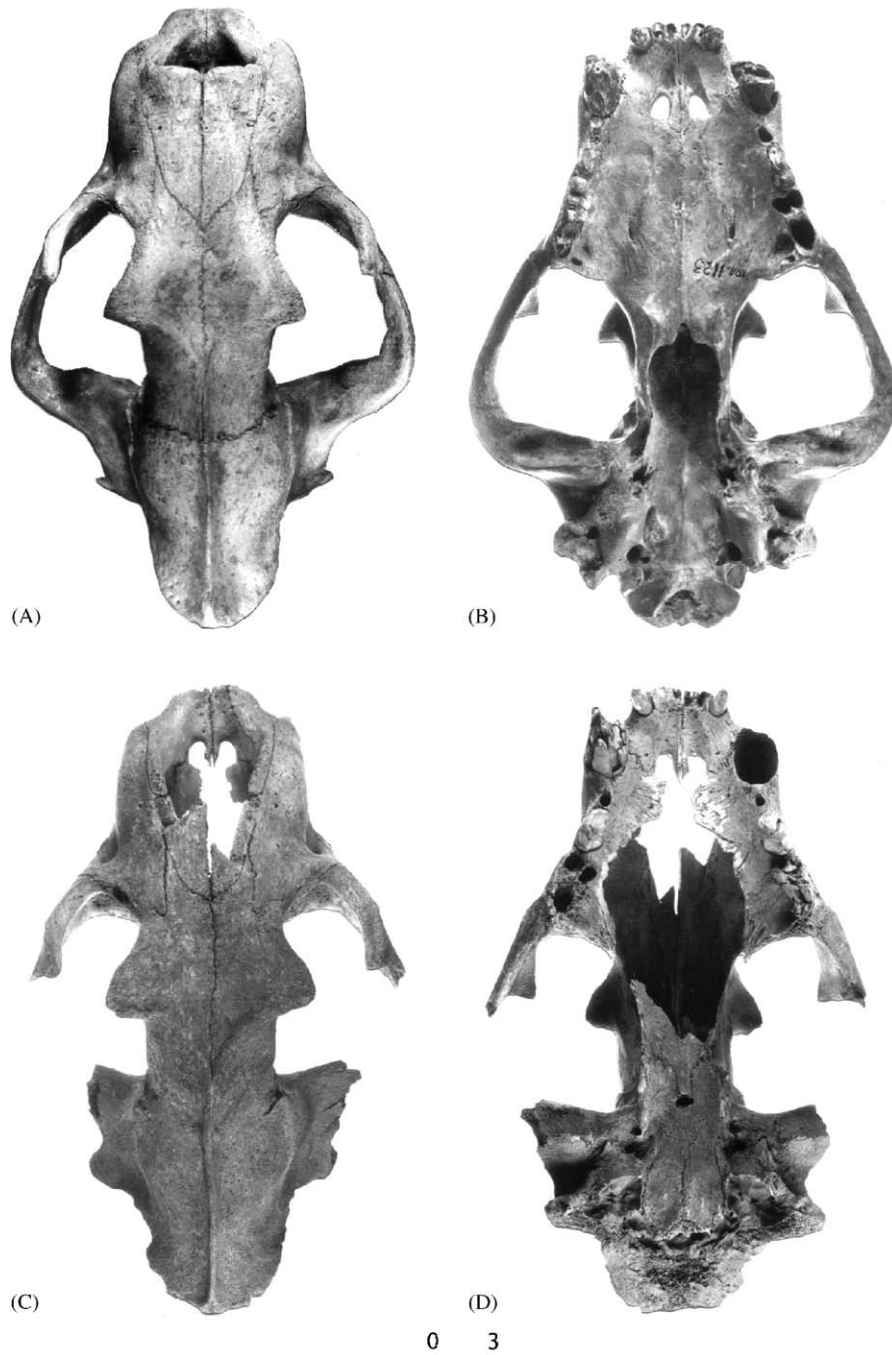


Fig. 2. *Panthera spelaea*. A,B—Skull GIN-1123, Smolensk: A—dorsal and B—ventral views. C,D—Skull IPBPS-1, Duvannyi Yar: C—dorsal and D—ventral views. Scale bar 30 mm.

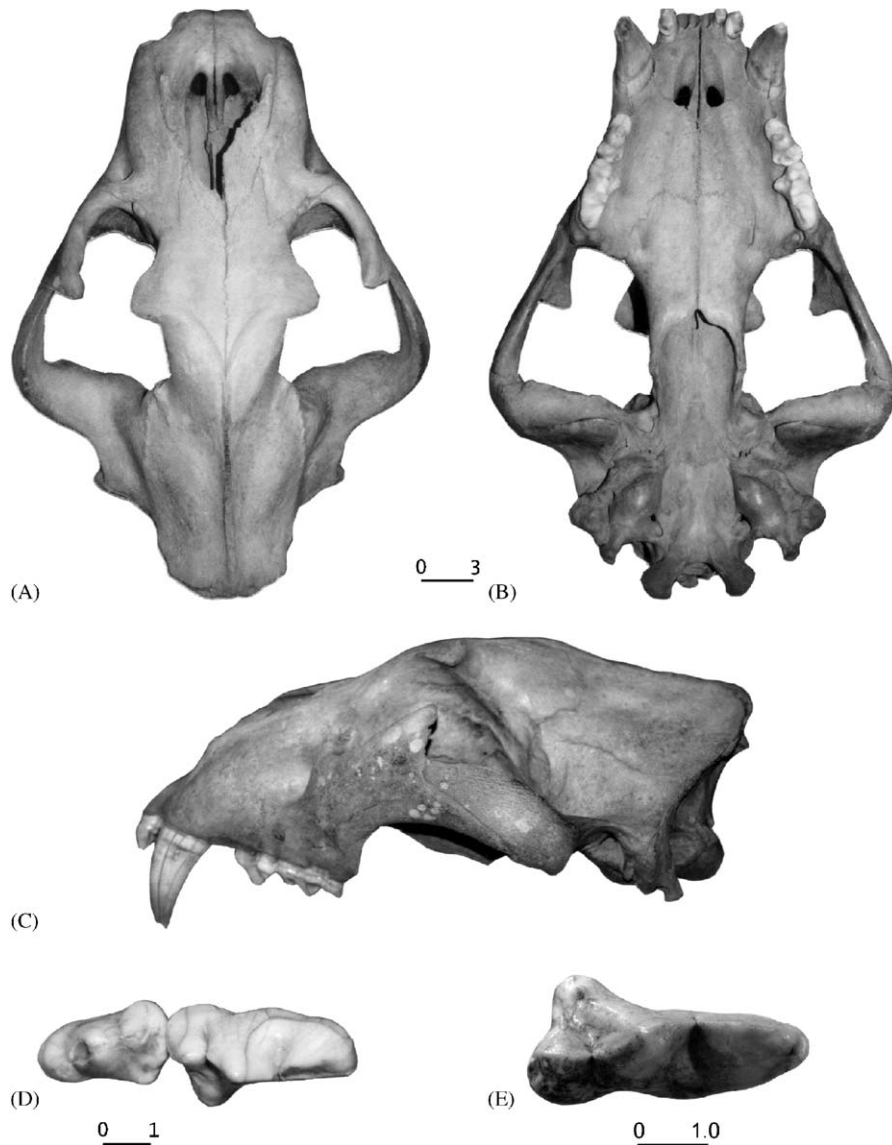


Fig. 3. *Panthera spelaea*. A–C—Skull K-1 (private collection), Kondakovka: A—dorsal, B—ventral, and C—lateral views. Scale bar 30 mm. D—Upper P3–P4 from skull K-1, Kondakovka: occlusal view. Scale bar 10 mm. E—Upper carnassial (P4) GIN/AV86-12, Avdeevo: occlusal view. Scale bar 10 mm.

Age: Late Pleistocene.

Description: According to the sizes of the upper canines all studied skulls derive from males (Table 1). Their basal cranial lengths range within limits known for male skulls of Eurasian *P. spelaea* (Fig. 4; Tables 2 and 3).

The principal cranial characters found in both European and Northern Siberian samples are wide muzzle, especially over the canines and P2 roots, relatively short facial part, short and wide nasals, rounded openings of the incisive foramina, sharply pointed posterior tip of the frontal process of maxillary bone, linear configuration of the zygomatic-maxillary suture, moderately arched zygoma, relatively elongated postorbital or cranial portion, narrow intertemporal region and braincase, slightly inflated bulla, widely separated posterior lacerate and condyloid foramina,

posteriorly expanded paroccipital processes, and large and laterally widened mastoid processes.

Among the tooth characters the most significant are: incisors with well-developed lingual cingulum, upper canines with slight lateral compression, upper carnassial lacking or with slightly developed small cingular preparastyle, large parastyle, and protocone bulge having the clear trend to lose the protocone cusp (Fig. 3D,E, Figs. 5D,E and 6D,E).

4. Comparison with *Panthera tigris*

As mentioned by earlier workers, the Late Pleistocene lion differs from the living tiger in many cranial characters: less arched skull, shorter and broader nasal

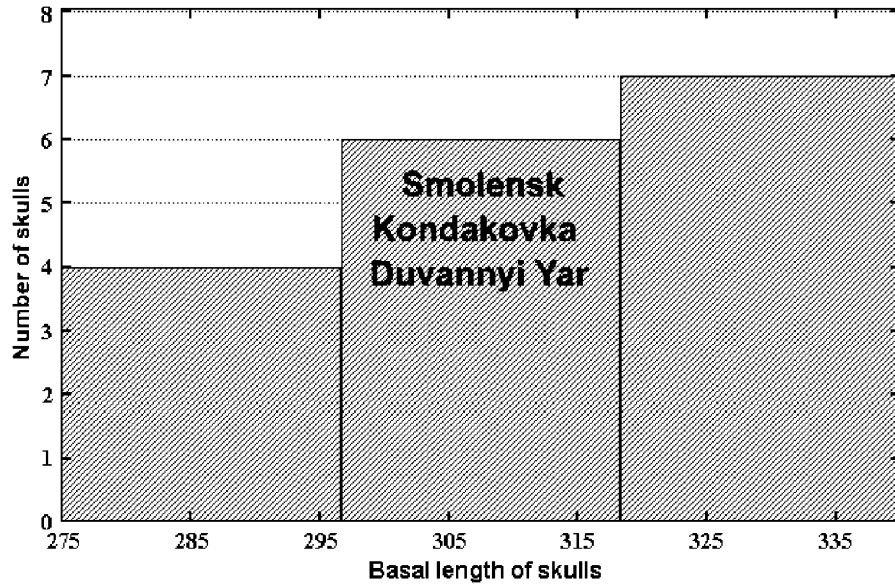


Fig. 4. Histogram of basal lengths of 17 skulls of Eurasian male *Panthera spelaea*. Data from Vereshchagin (1971), Baryshnikov and Boeskorov (2001), and this paper.

Table 1
Upper tooth measurements of *Panthera spelaea*

Measurements	K-1 Kondakovka Kolyma left	IPBPS-1 Duvanniy Yar Kolyma left	GIN-1123 Smolensk Russian Plain left	GIN/AV86-12 Avdeevo Russ. Plain right	F: AM 69048 Flat Creek Alaska right	F: AM 30751 Gold Stream Alaska right
I1 l/w	10.0al/-	–	9.2al/-	–	–	9.2/6.2
I2 l/w	12.0al/-	11.0al/-	12.1al/-	–	–	10.6/8.5
I3 l/w	14.3/11.4	13.0/11.2	13.0/10.5	–	–	13.7/11.2
C l/w	28.7/19.5	31.5/25.0	28.1/20.5	–	29.5/21.2	28.4/21.2
P2 l/w	7.7al/-	9.0al/-	8.8al/-	–	9.0al/-	7.0al/-
P3 l/w	28.0/16.3	24.5/14.4	25.0/-	–	26.5/14.7	26.2/15.2
P4 l/w	40.0/20.8	34.0al/-	35.0al/-	41.1/21.0	36.9/19.5	39.5/19.9
M1 l/w	-/12.0al	–	9.8al/-	–	-/11.0al	-/11.0 al

l—length; w—width; al—alveolar.

Table 2
Skull measurements used in ratio diagrams of various samples of *Panthera*

Measurements	<i>P. spelaea</i> K-1 Kondakovka Kolyma	<i>P. spelaea</i> IPBPS-1 Duvanniy Yar Kolyma	<i>P. spelaea</i> GIN-1123 Smolensk Russian Plain	<i>P. spelaea</i> F: AM 30460 Alaska	<i>P. spelaea</i> F: AM 69048 F. Creek Alaska	<i>P. spelaea</i> F: AM 30751 G. Stream Alaska	<i>P. fossilis</i> Azé, France (Argant, 1988)	<i>P. leo</i> ZMSU S-1639
LBa	305.0	307.0 ca.	309.0	306.0	301.0	292.0	347.7	315.0
LPN	160.0	160.0	165.0	–	–	–	172.6	175.0
LPO	140.0	140.0	140.0	133.5	145.0	–	162.5	152.0
WCa	103.0	105.0	107.0	110.2	102.4	100.5	112.3	98.0
WIO	72.0	76.5	75.5	77.4	80.0	77.5	93.0	76.5
WIn	47.0	51.5	46.5	51.9	49.2	49.1	49.0	51.5
WMa	153.0	152.0	146.0	143.5	150.8	154.4	162.5	137.0
WBu	26.5	–	25.8	31.5	32.0	32.0	34.0	36.0
WP2	77.0	76.0	82.0	79.0	74.2	72.5	85.0 ^a	72.0

Abbreviations as in Fig. 7.

^aMeasured from Fig. 1 (Argant, 1988)*.

Table 3
Measurements of new skulls of *Panthera spelaea* from the Russian plain and Siberia

Measurements	K-1, Kondakovka Kolyma	IPBPS-1, Duvanniy Yar, Kolyma	GIN-1123, Smolensk Russ. Plain
Greatest length	345.1	359.4	360.0
Condylbasal length	326.2	–	328.0
Palatal width between canines	57.5	57.0	62.5
Width in postorbital constriction	62.0	67.1	65.5
Zygomatic width	249.0	–	238.2
Greatest width across condyles	69.5	–	66.2
Greatest height in postorbital processes	120.3	–	128.1

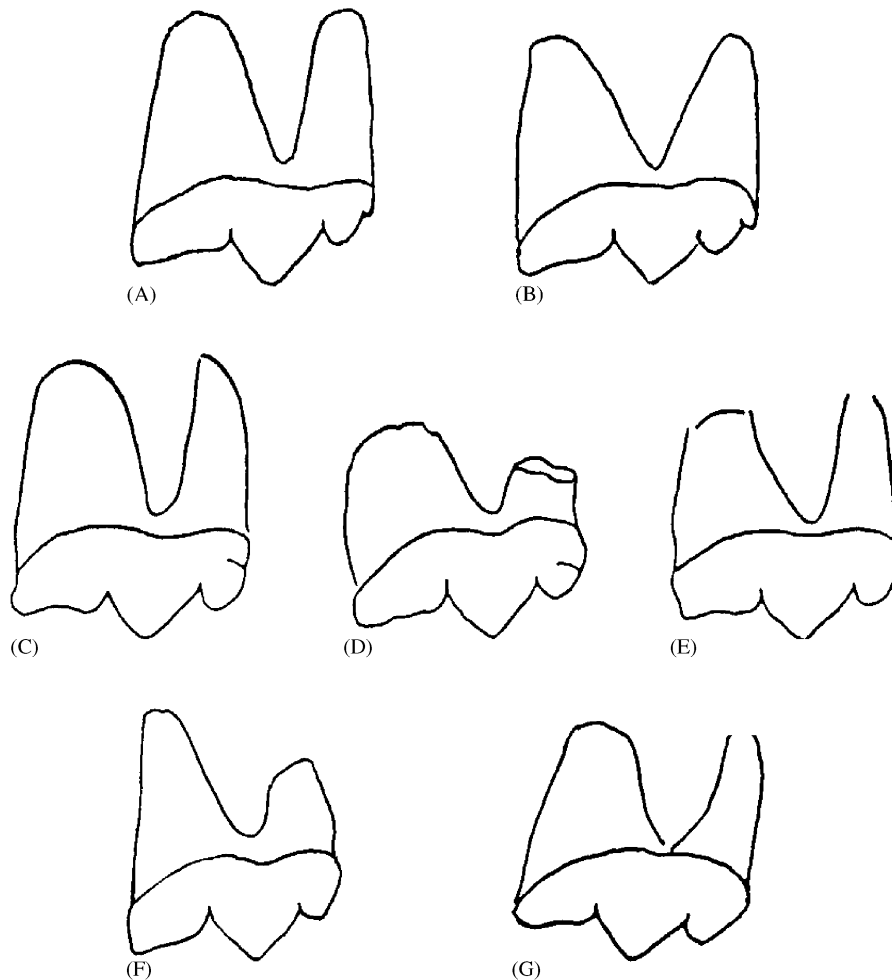


Fig. 5. Upper carnassials of *Panthera* sp., lateral views. A—*Panthera leo*; B—*Panthera tigris*; C–E—*Panthera spelaea*: C—Abimes de la Fage, France, after Ballesio (1975, Pl. 2, Fig. 2a); D—Avdeevo, European Russia; E—Kondakovka, North-Eastern Russia; F–G—*Panthera fossilis*: F—Isernia la Pineta, Italy, after Sala (1990, p. 191, Fig. 3); G—Mauer, Germany, after (Freudenberg, 1914, p. 639, Fig. 63). Scale bar 40 mm.

bones, acute end to the frontal process of the maxillary bone, and shorter postorbital part of the skull (Merriam and Stock, 1932).

Our comparison reveals advanced features of *P. tigris* relative to *P. spelaea*. These are the more complex form of the maxillary-zygomatic suture, sagittal crest with

posterior dorsal margin elevated up to the nuchal line, posterior lacerate and condyloid foramina located in one depression, P4 with well-developed preparastyle (Fig. 6B), and relatively reduced M1.

In its turn, *P. tigris* retains some primitive conditions, e.g., elongate elliptic incisive foramina, narrow palate,

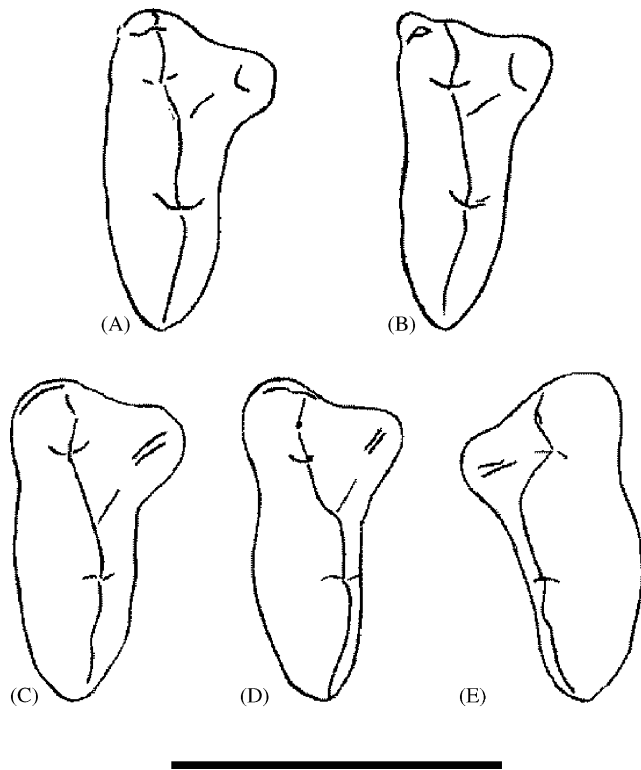


Fig. 6. Upper carnassial of *Panthera* sp, occlusal view. A—*Panthera leo*; B—*Panthera tigris*; C–E—*Panthera spelaea*: C—Abîmes de la Fage, France, after Ballesio (1975, Pl. 2, Fig. 4b); D—Avdeevo, European Russia; E—Kondakovka, North-Eastern Russia. Scale bar 40 mm.

especially between P2's, transversally narrow infraorbital foramina, relatively slightly inflated braincase area and bullae.

In cranial characters, *P. spelaea* and *P. tigris* share narrow braincase regions, relatively elongated postorbital constrictions, and relatively slight inflation of bullae. All these features are primitive within felids.

5. Comparison with *Panthera leo*

P. leo and *P. spelaea* share numerous characters, known to all students of this group of felids. We consider only one common character, the wide separation of the posterior lacerate and condyloid foramina, that points to their more primitive condition relative to most recent felids.

The living lion is advanced relative to *P. spelaea* in markedly more inflated bullae and braincase regions, strongly arched zygomata, a relatively short postorbital constriction, P3s with more developed additional posterior second cusp and upper carnassials P4s with preparastyles (Fig. 6A).

Alternatively, *P. spelaea* has some features that seem more advanced than the conditions seen in the living

lion. These are the widened muzzle in the canine and P2 areas, wide nasal bones, relatively short facial part of the skull, laterally widened mastoid area, V-shaped form of the posterior tip of the frontal process of maxillary bone, and reduced cusp on the protocone bulge of P4 (Fig. 6C–E). The ratio diagram (Fig. 7) shows a more significant proportional differentiation between the studied samples of *P. spelaea* and living *P. leo*.

Both *P. leo* and *P. spelaea* are advanced relative to tigers in their large and circular incisive foramina, larger and wider external nares, more acutely pointed frontal processes of the maxillae, larger postorbital processes and broader nasal bones.

6. Comparison with *Panthera atrox*

Comparison with the skulls of fossil lions in the Frick Collection of the American Museum of the Natural History—F:AM 30460, 69048 and 30751 (all from adult males) showed nearly identical morphology of Eurasian and Alaskan samples. Only a single external morphological character was found, namely, that the posterior palatine foramina are always located level with the posterior edges of P4s in all the American skulls examined while it is variable in position in the Eurasian specimens. In metric characters the first group of fossil lions demonstrates a slightly broader infraorbital region and wider bullae (Fig. 7).

Complete cranial specimens of the American Alaskan fossil lion and of the lion from the Central Plains of North America are poorly described in literature. There is information on only two complete skulls from the Yukon Territory (C.R. Harrington's data in Baryshnikov and Boeskorov, 2001), and a description of a skull from north-central Wyoming (Martin and Gilbert, 1978). Unfortunately, all derive from females and could not be used for this comparison. Most of our understanding of cranial characters of American *P. atrox* is based on the large population of fossil lions from Rancho La Brea. According to Merriam and Stock (1932) there is a close affinity between Eurasian and American forms. However, judging from their description, the Rancho La Brea lion can be distinguished from *P. spelaea* by its larger size, greater breadth across the postorbital constriction, trends for a third lingual root on the P3s, a single rooted condition in M1s, and for the posterior lacerate and condyloid foramina to be located within a single depression. All these features of the Rancho La Brea lion are likely derived.

7. Comparison with *Panthera fossilis*

The upper carnassial P4 of *P. spelaea* was compared with that of the lion-like *P. fossilis* from the early

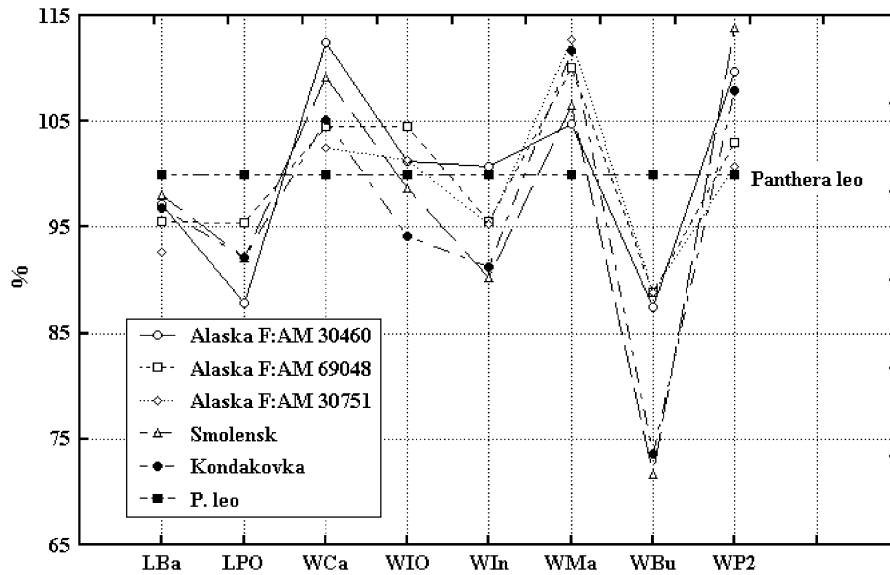


Fig. 7. Ratio diagram of cranial measurements of Late Pleistocene Eurasian and Alaskan fossil lions compared with *P. leo*. LBa—basal cranial length; LPN—length from prosthion to the posterior end of nasals; LPO—length from prosthion to the anterior margin of orbit; WCa—greatest base canine width; WIO—minimum infraorbital width; WIn—width across incisors row; WMa—greatest mastoid width; WBU—bulla width; WP2—palate width between P2.

Middle Pleistocene locality of Isernia la Pineta in Southern Italy and with that from Mauer, the type locality, late Middle Pleistocene of Germany. The upper carnassial of *P. fossilis* is characterized by a relatively small parastyle closely appressed to the paracone. There is no sign of a preparastyle on P4 (Fig. 5F,G). The upper carnassial of the cave lion is advanced relative to that of *P. fossilis* in having a larger parastyle better separated from the paracone. In addition, in *P. spelaea*, in distinction from *P. fossilis*, P4 tends to have an incipient cingulum anterior to the preparastyle.

Skulls of Middle Pleistocene lions are known from the Petralona Cave and from Mauer though they have not been completely described (Freudenberg, 1914; Kurtén and Poulianos, 1977). That is why we used the complete skull from the cave of Azé (Middle Pleistocene of France), described in detail by Argant (1988, 1991) as *P. spelaea* for the comparison. Here we assign this specimen to *P. fossilis*. This skull is very large and shares the same lion characters as both *P. leo* and *P. spelaea*. But the Azé skull demonstrates a more primitive condition in its very small incisors, relatively small orbits, less inflated bullae, and a relatively broader nuchal surface. In these features it differs from all above discussed members of the genus *Panthera*.

On the contrary, as compared to *P. spelaea*, *P. fossilis* exhibits proportions, which are more common with living pantherine cats. Namely, its cranial width is slightly narrower over the canine, P2's, and in the mastoid area (Fig. 8).

8. Discussion

The large lion-like cat *P. spelaea* is one of the important members of the Mammoth Steppe Fauna. It was widespread during the Late Pleistocene in Eurasia. The closely related lion-like *P. atrox* was nearly coeval in North America.

The history of lion-like cats dates from the Villafranchian with the earliest record in the African locality of Laetoli at ca. 3.5 Ma (Turner, 1990). The earliest European occurrence of lion-like *P. fossilis* is established in the Italian site Isernia la Pineta dated at about 0.7 Ma (Sala, 1990). This large fossil lion is poorly represented in the European record and is so far unknown in Asia. Its Middle Pleistocene history is inadequately studied. Unambiguous remains of *P. fossilis* are known in the Mosbach main fauna and from Mauer (Schütt and Hemmer, 1978). Besides, it is not impossible that other Middle Pleistocene European lion-like cats, for example from Château and Lunel-Viel (*P. spelaea* in Argant, 1980 and Bonifay, 1971) belong to the same species. On the other hand, it is still unclear when true *P. spelaea* appeared in Eurasia. For instance, a carnassial from Abîmes de la Fage, France, dated as Riss by Ballesio (1975), resembles a P4 of *P. spelaea* rather than of *P. fossilis* from Isernia or Mauer (Fig. 5). The well preserved Middle Pleistocene skull from Azé, also in France, is very different from the typical form of Late Pleistocene *P. spelaea*, and evidently belongs to *P. fossilis*.

According to the analyses of Schütt (1969), and Schütt and Hemmer (1978), the Middle Pleistocene lion

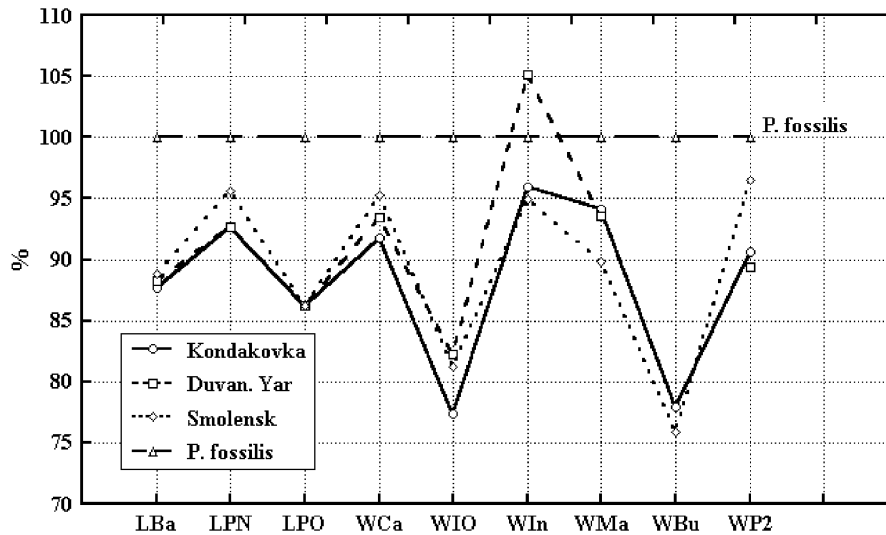


Fig. 8. Ratio diagram of cranial measurements of *Panthera spelaea* and *P. fossilis*. Abbreviations as in Fig. 7.

was larger and had less specialized lower teeth than *P. spelaea*. Our cranial analysis confirmed these results: the skull from Azé is larger and less specialized in its cranial characters compared to the Late Pleistocene *P. spelaea*. Among the primitive features of *P. fossilis* from Azé, the most significant is the small size of the incisive tooth row. Very small upper incisors occurred in ancient felids like *Pseudaehurus*: they were also small in *Therailurus*. As compared with our samples of cave lion, the difference in incisor size of Azé specimen is clearly seen in the ratio diagram (Fig. 8).

Schütt and Hemmer (1978) traced the evolutionary changes in teeth characters from *P. fossilis* to *P. spelaea* and considered the Middle Pleistocene large pantherine cat to be an ancestral form to the Eurasian cave lion. Our data does not contradict this viewpoint.

The systematic position of the Eurasian cave lion had long been debated. Most workers, especially those who dealt with the cranial material, have suggested relationships between the European cave lion and North American *P. atrox* with living *P. leo* (Merriam and Stock, 1932; Terzea, 1965; Vereshchagin, 1971; Martin and Gilbert, 1978; Argant, 1988; Baryshnikov and Boeskorov, 2001). The conception of a single species, *P. leo*, for all lion-like cats was accepted by Kurtén (1968, 1985), Hemmer (1967, 1974), Turner (1984), Turner and Antón (1997). Turner (1984, p.1) explained the difference within the group of Pleistocene and recent lions by the high level of their sexual dimorphism: he wrote “the felid, often referred to as the cave lion, appears to have been no more than a large, sexually dimorphic representative of the extant lion, *P. leo*”. In an earlier publication Vereshchagin (1971) had noted the advanced condition of cranial morphology in the cave lion relative to the living form and concluded that its subspecific status within *P. leo* is not correct. In spite

of this conclusion, Hemmer (1974), in his fundamental study of the systematic position of *P. leo* placed the Late Pleistocene cave lion within this species. However this opinion is generally based on the statistical study of different features, especially of teeth, and was poorly supported by the analysis of cranial characters of the fossil samples.

The analysis of skull characters showed that *P. spelaea* is a distinct species. Though *P. leo* is advanced compared to the cave lion in many aspects of cranial morphology (see the comparative study above), *P. spelaea* also possesses many other advanced characters relative to *P. leo* which support their separate evolution within the lion group.

Recent molecular data provide additional proof that the cave lion was highly distinct from its living relatives. According to Burger et al. (2004) the European lions of the *spelaea* group were isolated from their African and Asian relatives since the dispersal of lion-like forms to Eurasia in the early Middle Pleistocene.

The North American fossil lion *P. atrox* and the Eurasian cave lion share most features that were listed during the description of *P. spelaea* samples. Our study of Alaskan skulls showed its close affinity. We agree with Harington (1969), Vereshchagin (1971), Kurtén (1985), and Baryshnikov and Boeskorov (2001) in assigning the northwestern North American Late Pleistocene lions to the Eurasian species *P. spelaea*. But we did not find any differentiating characters in cranial morphology between both western and eastern Beringian fossil lions and other Eurasian samples of *P. spelaea*. Moreover B. Kurtén’s (1985) opinion on the relatively smaller size of the Beringian lion and his idea of subspecific separation of Arctic Siberian and Alaskan Late Pleistocene lions from *P. spelaea* on the base of size differences, recently discussed by Baryshnikov and

Boeskorov (2001), are not supported by our dimensional study of the cranial material from Beringia (Fig. 4, Table 2).

The final problem concerns the relationship of tigers and lions. On the basis of morphological, ethological, and physiological features Hemmer (1974, 1981) pointed out two distinct clades within the living large cats of the genus *Panthera*. In his opinion lions, leopards and jaguars demonstrate a clear set of common characters and can be separated from the second branch of large cats represented by the tiger. Molecular data also support the idea of the early separation of tigers from other pantherine cats (Janczewski et al., 1995) and demonstrates the relatively distant relationships of lions and tigers, whereas the tiger and jaguar show closer relations (Mattern and McLennan, 2000).

However, recently the discussion concerning relationships of the tiger and cave lion was re-opened by Groiss (1996) on the base of the analysis of brain morphology of *P. spelaea* from the Franconian cave of Germany. This author pointed to the tiger's type of brain of this specimen as well as of brains of *P. fossilis* and *P. atrox* and assigned the cave lion to *Panthera tigris spelaea*. Actually, there is a difference between the endocast of the brain of the fossil lion *P. atrox* and the living *Panthera*, which was mentioned by Merriam and Stock (1932). However, as was pointed out in the cranial analysis, tigers and fossil lions retained several primitive conditions including their slightly inflated braincase area and their similarities in the brain structure apparently may be interpreted as a shared plesiomorphic condition.

The distinct separation of tigers from lions on the basis of cranial characters was demonstrated in the comparative part of this study. We did not find any synapomorphies in their cranial structure which can support the close relationships of tigers and cave lions within the genus *Panthera*. In the light of the discussed morphological data as well as the data obtained by ethological, physiological, and molecular study we believe that the attribution of the fossil lions to tigers is unsupported by the factual evidence.

Acknowledgements

We are very grateful to Dr. A. S. Kremen' from the Smolensk State Pedagogical University and Dr. S. V. Gubin from Institute of Physicochemical and Biological Problems in Soil Science (Pushino) for bringing us the cave lion materials for our study. Our thanks are to all the colleagues and curators of mammalian collections who gave us access to their material, especially to Dr. R. Tedford and Mrs. Denny Diveley for the permission to study Alaskan skulls of fossil lions from the Frick Collection of AMNH. We are also grateful to the organizing committee of the Alaskan Workshop Meet-

ing (USA, Fairbanks, May, 2003) and 3rd International Mammoth Conference (Canada, Yukon, May, 2003) for the financial support, which provided a chance to study collections of University of Alaska Museum (Fairbanks) and American Museum of Natural History (New York). Cordial thanks go to reviewers Harold Bryant and Rufus Churcher for their helpful remarks on the manuscript and for careful correction of the English text. The work was also supported by the grant RFBR 02-05-641.

References

- Altuna, J., 1981. Fund eines Skeletts des Höhlenlöwen (*Panthera spelaea* Goldfuss) in Arrikruz, Baskenland. Bonner zoologische Beiträge 32 (1–2), 31–46.
- Argant, A., 1980. Une brèche fossilifère du Pléistocène moyen de Saône-et-Loire: étude paléontologique du gisement de Château. Memoire l'Universite Claude Bernard – Lyon 1 81, 2–144.
- Argant, A., 1988. Etude de l'exemplaire de *Panthera spelaea* (Goldfuss, 1810) (Mammalia, Carnivora, Felidae) du gisement Pléistocène moyen récent de la Grotte d'Azé (Saone et Loire). Revue de Paléobiologie 7 (2), 449–466.
- Argant, A., 1991. Carnivores quaternaires de Bourgogne. Documents des Laboratoires de Géologie. Lyon 115, 1–301.
- Ballesio, R., 1975. Etude de *Panthera (Leo) spelaea* (Goldfuss) nov. sub. sp. (Mammalia, Carnivora, Felidae) du gisement Pléistocène moyen des Abîmes de la Frage à Noailles (Corrèze). Nouveau Archive Muséum Histoire Naturelle 13, 47–55.
- Baryshnikov, G., Boeskorov, G., 2001. The Pleistocene cave lion, *Panthera spelaea* (Carnivora, Felidae) from Yakutia, Russia. Cranium 18 (1), 7–23.
- Beaumont, G.de, 1964. Remarques sur la classification des Felidae. Eclogae Geologicae Helvetiae 57 (2), 837–845.
- Bonifay, M.F., 1971. Carnivores quaternaires du Sud-Est de la France. Mémoires du Muséum National d'Histoire Naturelle, Nouvelle Série C. 21 (2), 43–377.
- Burger, J., Rosendahl, W., Loreille, O., Hemmer, H., Eriksson, T., Götherström, A., Hiller, J., Collins, M.J., Wess, T., Alt, K.W., 2004. Molecular phylogeny of the extinct cave lion *Panthera leo spelaea*. Molecular Phylogenetics and Evolution 30, 841–849.
- Dietrich, W.O., 1968. Fossile Löwen im europäischen und afrikanischen Pleistozän. Palaeontologische Abhandlungen. Abteilung A–Paläozoologie 3 (2), 193–366.
- Flynn, J.J., Galiano, H., 1982. Phylogeny of Early Tertiary Carnivora, with a description of a new species of *Protictis* from the Middle Eocene of northwestern Wyoming. American Museum Novitates 2725, 1–64.
- Freudenberg, W., 1914. Die Säugetiere des älteren Quartärs von Mitteleuropa. Geologische und Palaeontologische Abhandlungen 12 (4–5), 1–219.
- Groiss, J., 1996. Der Höhlentiger *Panthera tigris spelaea* (Goldfuss). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 7, 399–414.
- Harrington, C.R., 1969. Pleistocene remains of the lion-like cat (*Panthera atrox*) from the Yukon Territory and northern Alaska. Canadian Journal of Earth Sciences 6 (5), 1277–1288.
- Hemmer, H., 1967. Wohin gehört "Felis" palaeosinensis Zdansky, 1924 in systematischer Hinsicht? Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen 129 (1), 83–96.
- Hemmer, H., 1974. Untersuchungen zur Stammesgeschichte der Pantherkatzen (Pantherinae). Teil III. Zur Artgeschichte des Löwen, *Panthera (Panthera) leo* (Linnaeus 1758). Veröffentlichungen der Zoologischen Staatssammlung 17, 167–280.

- Hemmer, H., 1981. Die Evolution der Pantherkatzen: Modell zur Überprüfung der Brauchbarkeit der Hennigschen Prinzipien der Phylogenetischen Systematik für wirbeltierpaläontologische Studien. *Paläontologische Zeitschrift* 55 (1), 109–116.
- Janczewski, D.W., Modi, W.S., Stephens, J.C., O'Brien, S.J., 1995. Molecular evolution of mitochondrial 12S RNA and cytochrome b sequences in the pantherine lineage of Felidae. *Molecular Biology Evolution* 12 (4), 690–707.
- Kurtén, B., 1968. Pleistocene mammals of Europe. Weidenfeld and Nicolson. London. 317 pp.
- Kurtén, B., 1985. The Pleistocene lion of Beringia. *Annales Zoologici Fennici* 22, 117–121.
- Kurtén, B., Poulianos, N., 1977. New stratigraphic and faunal material from Petralona Cave with special reference to the Carnivora. *Anthropos* 4 (1–2), 47–130.
- Martin, L. D., 1997. Felidae. In: Janis, C. M., Scott K. M., Jacobs L. L. (Eds.), *Evolution of Tertiary Mammals of North America. Volume 1: Terrestrial Carnivores Ungulates, and Ungulate-like Mammals*. Cambridge University Press. pp. 236–242.
- Martin, L.D., Gilbert, B.M., 1978. An American lion *Panthera atrox*, from Natural Trap Cave, North Central Wyoming. *Contributions to Geology, University of Wyoming* 16 (2), 95–101.
- Mattern, M.Y., McLennan, D.A., 2000. Phylogeny and speciation of felids. *Cladistics* 16, 232–253.
- Merriam, J.C., Stock, C., 1932. The Felidae of Rancho La Brea. *Carnegie Institution of Washington Publications* 442, 1–231.
- Sala, B., 1990. *Panthera leo fossilis* (v. Reich., 1906) (Felidae) de Isernia la Pineta (Pléistocène moyen inférieur d'Italie). *Geobios* 23 (2), 189–194.
- Schütt, G., 1969. Untersuchungen am Gebiss von *Panthera leo fossilis* (v. Reichenau, 1906) und *Panthera leo spelaea*. (Goldfuss, 1810). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 134 (2), 192–220.
- Schütt, G., Hemmer, H., 1978. Zur Evolution des Löwen (*Panthera leo* L.) im europäischen Pleistozän. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 4, 228–255.
- Simpson, G.G., 1941. Large Pleistocene felines of North America. *American Museum Novitates* 1136, 1–27.
- Terzea, E., 1965. *Panthera spelaea* (Goldf.) in pleistocenul superior din România. *Lucrarile Institutului de Speologie "Emil Racoviță" 4*, Bucuresti, pp. 251–283.
- Turner, A., 1984. Dental sex dimorphism in European lions (*Panthera leo* L.) of the Upper Pleistocene: palaeoecological and palaeoethological implications. *Annales Zoologici Fennici* 21, 1–8.
- Turner, A., 1990. The evolution of the guild of larger terrestrial carnivores during the Plio-Pleistocene in Africa. *Geobios* 23 (3), 349–368.
- Turner, A., Antón, M., 1997. *The big cats and their fossil relatives*. Columbia University Press, New York. 234 pp.
- Van Valkenburgh, B., Grady, F., Kurtén, B., 1990. The Plio-Pleistocene cheetah-like cat *Miracinonyx inexpectatus* of North America. *Journal of Vertebrate Paleontology* 10 (4), 434–454.
- Vereshchagin, N.K., 1971. The cave lion and its history in the Holarctic and on the territory of the U.S.S.R. *Trudy of Zoological Institute* 49, 123–199 Leningrad (in Russian).
- Wiszniowska, T., 1978. *Panthera spelaea* (Goldfuss) z Jaskini Niedźwiedziej w Kletnie. *Actauniversitatis Wratislaviensis*, 311, *Studia Geograficzne*. 24, Wrocław, 113–141 (in Polish).
- Wyss, A.R., Flynn, J.J., 1993. A phylogenetic analysis and definition of the Carnivora. In: Szalay, F.S., Novacek, M.J., McKenna, M.C. (Eds.), *Mammal Phylogeny*. Springer, New York, pp. 32–52.