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LATE PLEISTOCENE FELIDAE REMAINS (MAMMALIA, CARNIVORA) FROM GEOGRAPHICAL SOCIETY CAVE IN THE RUSSIAN FAR EAST

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ABSTRACT

Fossil remains of felids from Geographical Society Cave and neighboring localities (Tigrovaya Cave, Malaya Pensau Cave, and Letuchiya Mysh Cave) in the Russian Far East are found to belong to four species: *Panthera tigris*, *P. spelaea*, *P. pardus*, and *Lynx lynx*. In Geographical Society Cave, the felid fossils are confined to deposits of the warm stage of the Late Pleistocene (MIS3). The simultaneous presence of *Panthera tigris* and *P. spelaea* seems to be unusual, the tiger remains being numerous whereas those of the cave lion are scant. There are differences between the Late Pleistocene tiger and the recent tiger in dental characters. *P. tigris*, most probably, migrated twice to Russian Far East from southern regions: in interstadial MIS3 and, subsequently, in the Holocene.

Key words: evolution, Felidae, Late Pleistocene, Palaeolithic cave sites, Russian Far East

ПОЗДНЕПЛЕЙСТОЦЕНОВЫЕ ОСТАТКИ FELIDAE (MAMMALIA, CARNIVORA) ИЗ ПЕЩЕРЫ ГЕОГРАФИЧЕСКОГО ОБЩЕСТВА НА ДАЛЬНЕМ ВОСТОКЕ РОССИИ

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РЕЗЮМЕ

Установлено, что ископаемые остатки фелид из пещеры Географического общества и прилежащих местонахождений (пещеры Тигровая, Малая Пенсау и Летучая Мышь) на юге Дальнего Востока России принадлежат четырем видам: *Panthera tigris*, *P. spelaea*, *P. pardus* and *Lynx lynx*. В пещере Географического общества они обнаружены в отложениях теплой стадии позднего плейстоцена (MIS3). Необычно совместное присутствие *Panthera tigris* and *P. spelaea*, причем костные остатки тигра многочисленны, в то время как таковые пещерного льва редки. Имеются дентальные различия между тигром из позднего плейстоцена и современным тигром. *P. tigris*, скорее всего, расселялся на Дальний Восток России с юга дважды: в интерстадиале (MIS3) и затем в голоцене.

Ключевые слова: эволюция, Felidae, поздний плейстоцен, палеолитические пещерные стоянки, Дальний Восток России

INTRODUCTION

The mammal fauna in the southern part of the Russian Far East is complex. For example, the carnivore fauna includes boreal species near the southern border of their distribution ranges (*Martes zibellina* (L., 1758), *Gulo gulo* (L., 1758), as well as the representatives of subtropical and tropical regions there reaching the northern limits of their distribution in Eastern Asia (*Nyctereutes procyonoides* (Gray, 1834), *Ursus thibetanus* G.Cuvier, 1823, *Martes flavigula* (Boddaert, 1785), *Panthera tigris* (L., 1758), *P. pardus* (L., 1758), *Prionailurus bengalensis* (Kerr, 1792)). The history of the Late Pleistocene carnivore fauna

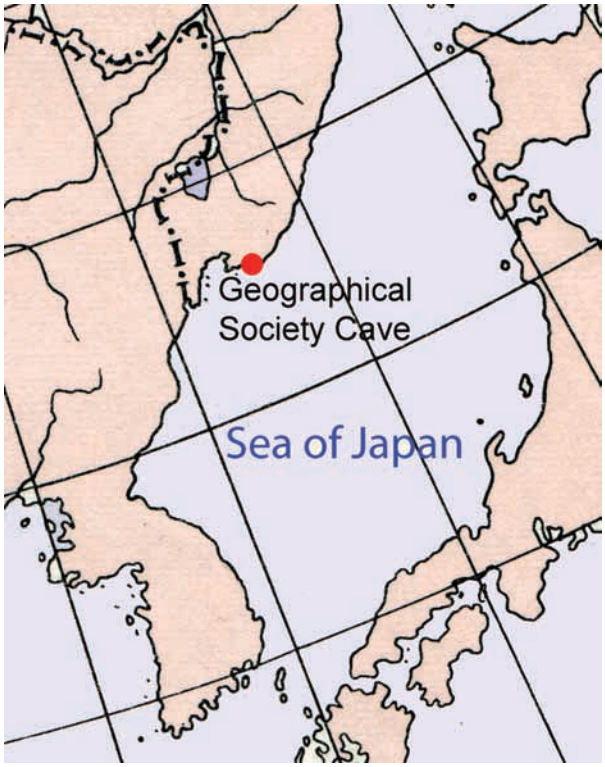

Fig. 1. Location of the cave.

remained unknown in the region for a long time. The first fossil remains of Carnivora were excavated in the Geographical Society Cave and in several adjacent small karst cavities of Tigrovaya Cave, Malaya Pensau Cave, Letuchaya Mysh, and Spyashchaya Krasavitsa, which are located in the valley of the Partizanskaya River (formerly Suchan River) near Nakhodka City in the Primorskii Territory (42°93´N; 133°05´E) (Fig. 1). The data on canids, ursids, mustelids, and hyenids from these collections have been already published by me (Baryshnikov 2014, 2015a, b). The present communication deals with the analysis of the felids.

Fossil bones and teeth of a large cat from the localities of the Russian Far East were examined for the first time by Vereshchagin (1971). He pointed out in his review of cave lion *Panthera spelaea* (Goldfuss, 1810) finds from the territory of the former USSR that caves in the valley of Partizanskaya River (former Suchan River) in the southern part of Primorskii Territory included mainly bone remains of the tiger (*Panthera tigris*), with sporadic findings of jaw fragments and teeth of the cave lion. In his opinion, Geographical Society Cave is unique in the former Soviet Union, where both species of these large cats had been found; however he did not distinguish or describe their remains. Ovodov (1977) included in his tentative checklist of the Late Pleistocene mammals from Geographical Society Cave (layers 4–5) *Prionailurus bengalensis* (1 bone), *Lynx lynx*, *Panthera tigris/spelaea*, and *P. pardus*.

The focus of the present study is a re-identification and morphological description of fossil felid material from Geographical Society Cave, Tigrovaya Cave, Malaya Pensau Cave and Letuchaya Mysh Cave, which is kept in Zoological Institute of the Russian Academy of Sciences in Saint-Petersburg (ZIN). This material comes predominantly from 1966–1967 excavations by N. Ovodov, supplemented with several findings by N. Vereshchagin in 1966 and by the local history researcher E. Leshok in 1972. I did not include *Prionailurus bengalensis* in this survey, since its relationship with the Pleistocene fauna seems to be unclear.

A detailed description of Geographical Society Cave has been earlier provided by me (Baryshnikov 2014). Most of the fossil finds have no stratigraphic position, being characterized only by their depth. However, Ovodov (1977) pointed out that osteological material is mainly associated with layer 4. This layer 0.6–1.0 m thick was also found to contain scarce stone artifacts testifying visits by ancient hominins (Okladnikov et al. 1968).

Five AMS ^{14}C dates were made on the tiger bones: 34,300±1,700 (AA-38229), 35,100±1,900 (AA-37069), >38,000 (AA-37071), >39,000 (AA-37068), >40,000 (AA-37070) (Kuzmin et al. 2001). In addition, six AMS ^{14}C dates, ranging from 34,510 to 48,650, were determined on the hyena bones (Kuzmin et al., 2001; Rohland et al., 2005; Stuart and Lister, 2014). Thus, so the evidence indicates that formation of the bone-bearing layer in Geographical Society Cave fell within a Late Pleistocene warm phase (MIS 3).

Institutional abbreviations. BM, Museum of the Czech Karst (Beroun City, Czech Republic); GMY, Geological Museum (Yakutsk, Russia); IEPA, Institute of Ecology of Plants and Animals (Russian Academy of Sciences, Ekaterinburg, Russia); MEU, Museum of Evolution (Uppsala, Sweden); MMY, Mammoth Museum (Yakutsk, Russia); NKHUB, Natural History Museum of Humboldt University (Berlin, Germany); NHMP, Natural History Museum (Prague, Czech Republic); ZIN, Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia).

Measurements. Dental measurements: *L* – greatest length, *Lmst* – length of metastylar blade, *Lpad* – length of paraconid, *W* – greatest width. Limb bones measurements: *Bd* – breadth of the distal end, *BG* – breadth of the glenoid cavity, *Bp* – breadth of the proximal end, *BPC* – breadth across the coronoid process, *Dd* –depth of the distal end, *Dp* – depth of the proximal end, *DPA* – depth across the Processus anconaeus, *GB* – greatest breadth, *GL* – greatest length, *GLP* – greatest length of glenoid process, *LAR* – length of the acetabulum on the rim, *SD* – breadth of the diaphysis in medium part, *SDO* – smallest depth of the olecranon, *SH* – smallest height of the shaft of ilium, *SLC* – smallest length of neck of the scapula. Measurements were taken in accordance with the scheme by von den Driesch (1968).

SYSTEMATICS

Family Felidae Fischer de Waldheim, 1817

Genus *Panthera* Oken, 1816

Panthera (*Tigris*) *tigris* (Linnaeus, 1758)

Ovodov (1977) counted 233 bone remains of a large cat from 5 individuals, which were assigned to *Panthera tigris* or *P. spelaea*. I calculated 211 tiger bones in the examined material, referring them to 6 individuals. By the number of bone remains of Carnivora from Geographical Society Cave, the tiger is second to the wolf (*Canis lupus* L., 1758).

Description and comparison. The tiger bone material is represented by mandible fragments, isolated teeth, and components of the postcranial skeleton. Fragments of vertebrae are scarce. The limb bones predominate; long bones being fragmented and short bones (carpals, tarsals, metacarpals, metatarsals and phalanx) remaining intact.

Mandibles. The collection from Geographical Society Cave contains a comparatively small fragment of left mandible (ZIN 34930-2) with the only tooth an m1 (Fig. 2C, D). The masseteric fossa is deep and extends only to the posterior margin of m1, which is characteristic of *P. tigris* (in *P. spelaea* and *P. leo* (L., 1758), the masseteric fossa stretches farther, reaching, as a rule, the level of the middle of the m1 crown).

More complete mandible fragments originate from the Pleistocene layers of Tigrovaya Cave and Malaya Pensau Cave, which are situated near the Geographical Society Cave. These mandibles are smaller than mandibles of *Panthera spelaea* males

Table 1. Measurements (mm) of mandibles of Late Pleistocene *Panthera tigris* and *P. spelaea* from the Russian Far East.

Measurements	*P. tigris*				*P. spelaea*	
	Geographical Society Cave	Tigrovaya Cave	Malaya Pensau Cave		Geographical Society Cave	
	ZIN 34930-3	ZIN 37295, sad	ZIN 37293	ZIN 37294	ZIN 37930	ZIN 34931
Total length		204.7				
Lc1-m1		119.0			128.0	
Lp3-m1	62.0	71.9	66.4	ca69.5	76.0	
Lp3-p4	38.6	45.6			45.0	
Height behind m1		40.5	52.9	50.1		38.3
Height before p3		48.0		49.6	51.3	
Teeth						
Lc1					26.1	
Wc1					19.0	
Lp3	15.6	19.1	16.7		18.4	
Wp3	8.3	9.6	8.0		10.4	
Lp4	23.6	26.4		23.7	27.8	
Wp4	–	13.2		11.8	13.1	
Lm1	26.3	28.6	28.1	28.3	ca28.6	24.6
Wm1	13.6	13.9	13.4	13.0	–	12.1

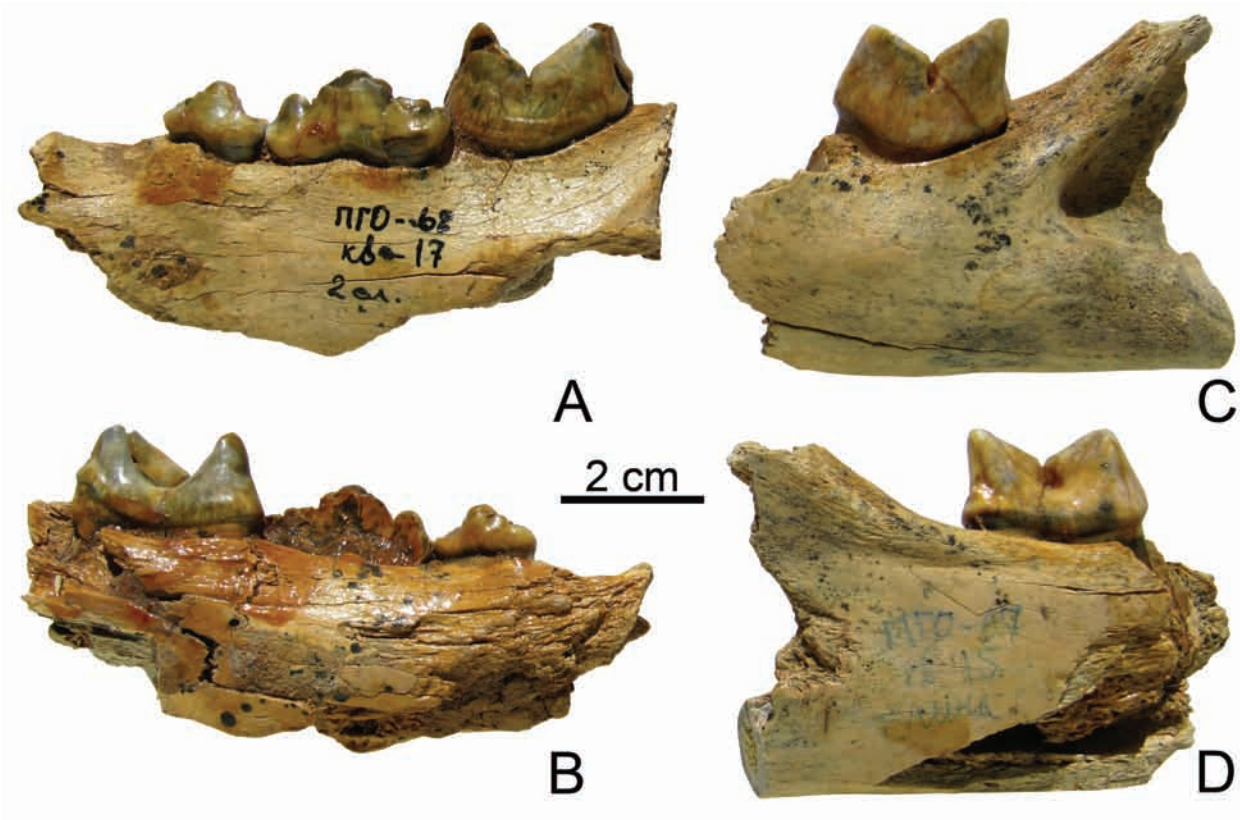

Fig. 2. *Panthera spelaea* (A, B) and *P. tigris* (C, D), Geographical Society Cave, mandible fragments; buccal (A, C) and lingual (B, D) views; A, B – ZIN 37931, left, with p3–m1; C, D – ZIN 34930-2, left, with m1.

(Table 1–3).The right mandible from Tigrovaya Cave (ZIN 37295; Fig. 3A, B) is referred to a subadult animal. The specimen is nearly complete p3–m1 and the alveolus of p2. The right mandible fragment (ZIN 37293; Fig. 3E, F) and left mandible fragment (ZIN 37294; Fig. 3C, D) recovered in Malaya Pensau Cave have no anterior portions; both bones may be referred to adult individuals. All specimens reveal the straight lower margin of the ramus as in *P. tigris* (in *P. leo* and *P. spelaea*, it is frequently convex at the level of m1; see Boule 1906, Ryabinin 1918, Vereshchagin 1971). Several jaws of the subspecies *P. spelaea vereshchagini* Baryshnikov et Boeskorov, 2001, described from Yakutia, also have the straight lower margin (for example, ZIN 29405 from Berezovka River, Kolyma River basin). The posterior portion of coronoid process is broken in mandibles from Tigrovaya Cave and Malaya Pensau Cave; presumably, it extended beyond the level of the articulatory process, as in *P. tigris* (the coronid process of *P. spelaea* generally does not extend beyond the level of the articulatory process). In the specimen ZIN 37295, the ramus height, measured in front of p3, exceeds the height measured behind m1; whereas the inverse dimensions are seen in ZIN 37294, similar to *P. spelaea vereshchagini* (see Baryshnikov and Boeskorov 2001, Boeskorov and Baryshnikov 2013). The masseteric fossa of the specimens from Tigrovaya Cave and Malaya Pensau Cave does not stretch forwards beyond the level of the posterior portion of m1 (as in the recent *P. tigris*).

Deciduous teeth. The Geographical Society Cave contained the fossil remains of tiger cubs including mandibular and maxillary fragments as well as isolated milk teeth, which belong to 3 individuals.

The left maxilla fragment with the alveolus of D2 and broken D3 (ZIN 34490-34) is present. The fragment of D3 is very high (crown buccal height measuring 9.4 mm). Its greatest width constitutes 10.3 mm. Two additional cuspids (parastyle and preparastyle) are placed in front of the main cusp. The

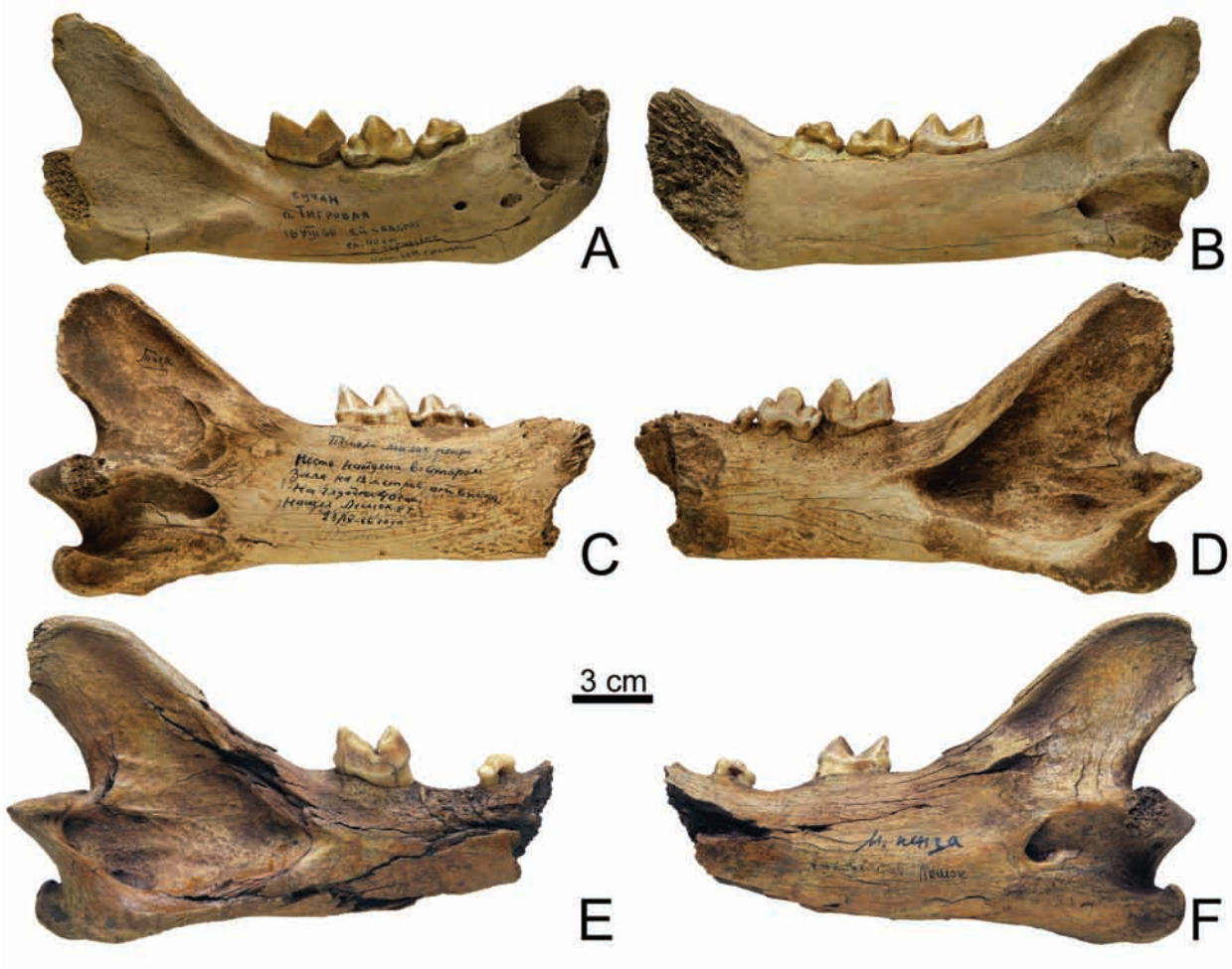

Fig. 3. *Panthera tigris*, Tigrovaya Cave (A, B) and Malaya Pensau Cave (C–F), mandibles; buccal (A, D, E) and lingual (B, C, F) views; A, B – ZIN 37295, right, subad.; C, D – ZIN 37294, left, ad.; E, F – ZIN 37293, right, ad.

inconspicuous protocone is located at the level of the peak of the main cusp.

There are three upper milk canines dC1 (the right and two left) and two right lower canines dc1 (Fig. 4A–H). All canines have roots and reveal no signs of resorption. Their dimensions and shape do not differ from the same milk teeth of the recent *P. tigris* (Table 4).

The right mandible fragment (ZIN 37288-3) has the alveolus of the deciduous canine as well as the alveolus of the unerupted permanent canine and a fragment of d3. The mandible height near the postcanine diastema is 27.6 mm.

The isolated right low d4 (ZIN 37288-76) does not differ in shape from that of recent *P. tigris*, although larger. The metaconid is large. The talonid has the form of a pointed cuspid, which is better developed in comparison with recent *P. leo* (Fig. 4K, L).

Permanent teeth. The upper dentition is represented by isolated incisors, canines, and several cheek teeth. The incisor I3 corresponds in size to recent *P. tigris* (Table 5).

There are four specimens of upper canine (C1). The outer (buccal) and inner (lingual) surfaces of the crown show two vertical grooves. The inner surface is flat and is separated from the convex outer surface by the sharp blade of the posterior part of the tooth. The height of enamel crown constitutes 47–49 mm.

The left canines are represented by the large specimen (ZIN 37288-35), presumably, from a male,

Table 2. Measurements (mm) of mandibles of Late Pleistocene *Panthera spelaea* from Europe.

Measurements	Males			Females		
	Germany				Czech Republic	
	Zoolithen Cave		Hermannshöhle	Lauchstädt	Svobodné Dvory Morávskova cihelna	Srbsko Chlum Komin Cave
	NKHUB 30073	NKHUB 48115.2	NKHUB 14298	NKHUB 30066	NHMP 26895	NHMP R4582
Total length			252.5	206.0		
Lc1-m1	ca135	134.1	ca126	111.3	122.0	106.9
Lp3-m1	80.4	75.6	75.5	66.6	70.9	64.5
Height behind m1	54.5	59.5		48.5		
Height before p3	56.1	53.8	50.0	43.8	47.9	
Teeth						
Lc1		26.1	–	–	23.5	22.0
Wc1		17.3	18.7	14.6	17.9	15.7
Lp3	20.8	18.3	19.0	17.0	17.4	15.7
Wp3	11.5	10.2	9.6	9.5	9.9	8.9
Lp4	29.9	26.3	27.6	25.4	25.3	24.2
Wp4	14.7	13.2	13.4	12.5	13.4	11.6
Lm1	31.7	30.3		27.5	29.4	27.6
Wm1	15.9	14.7		13.8	13.5	14.1

Table 3. Measurements (mm) of mandibles of Late Pleistocene *Panthera spelaea* from Siberia.

Measurements	*P. s. spelaea*				*P. s. vereshchagini*	
	Western Siberia				Eastern Siberia	
	Males			Female	Male	Female
	Krasnyi Yar, Ob River		Saltymakovo, Tom River	Krasnyi Yar, Ob River	Kurtak-4, Yenisei River	Berezovka River
	ZIN 32746-1	ZIN 32746-2	ZIN 32747	ZIN 32746-3	ZIN 36409	ZIN 329405
Total length	272.0	257.7	261.4		240.6	221.2
Lc1-m1	135.2	139.1	ca138	118.6	124.2	120.8
Lp3-m1	73.7	80.2	79.4	70.9	76.8	75.0
Lp3-p4	46.9	49.7	52.5	43.6	48.6	45.7
Height behind m1	56.9	54.9	57.8	48.9	54.8	49.5
Height before p3	51.4	56.4	54.3	45.1	53.9	44.8
Teeth						
Lc1	27.2	28.5		22.0	23.6	
Wc1	20.7	22.6		15.8	18.5	
Lp3	18.4	20.5		16.3		
Wp3	10.1	10.5		10.1		
Lp4	27.8	30.8	28.2	26.4	27.9	25.3
Wp4	11.8	15.3	13.4	12.6	13.6	12.7
Lm1	ca28.0	32.2		ca26.7	29.9	28.6
Wm1	13.7	15.7		13.5	14.8	14.4

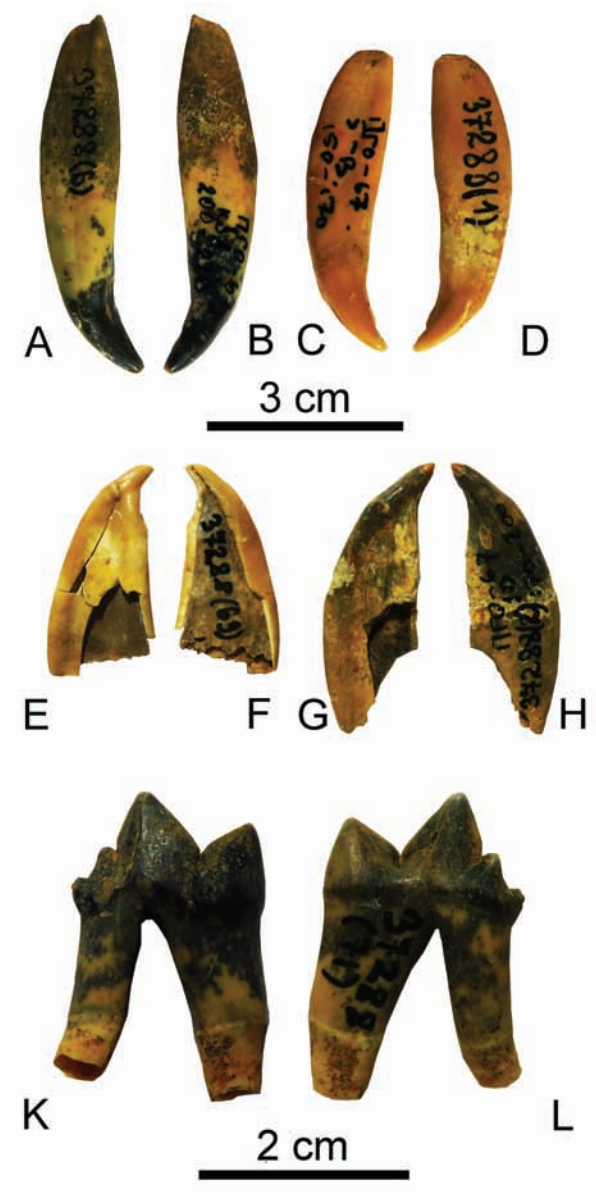

Fig. 4. *Panthera tigris*, Geographical Society Cave, milk teeth; buccal (B, C, F, H, K) and lingual (A, D, E, G, L) views; A, B – ZIN 37288-6, right; C, D – ZIN 37288-1, left; E, F – ZIN 37288-69, right; G, H – ZIN 37288-2, right; K, L – ZIN 37288-71, right.

and the smaller one (ZIN 37288-61), which is probably a female. Both right canines (ZIN 37288-28, 37288-29) are characterized by heir comparatively small size (Table 5). Two additional canines (presumably belonging to male and female) were found in the neighboring caves of Tigrovaya and Letuchaya Mysh. Therefore, female canines predominate in the

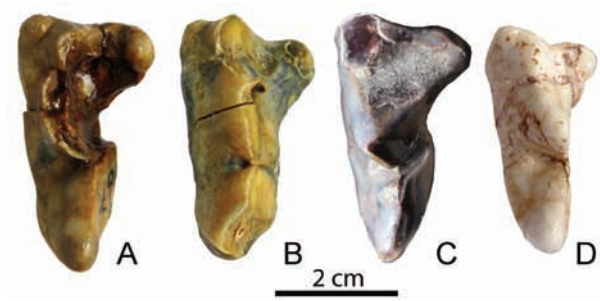

Fig. 5. *Panthera tigris* (A–C) and *P. palaeosinensis* (D), upper P4, Geographical Society Cave (A, B), Trinil, Indonesia (C) and Henan (Locality 39), China (D); occlusal view; A – ZIN 37288-4, right, def.; B – ZIN 37288-114, right; C – NKHUB 30002, right (type of *Feliopsis palaeojavanica* Stremme, 1911); D – MEU M3656, holotype.

examined material. These teeth correspond in size to the female teeth of the recent subspecies *P. tigris altaica* (Temminck, 1844) which occurs in Primorskii Territory.

The upper cheek teeth are represented by one P2 and two P4 (Fig. 5A, B). The premolar P2 (ZIN 37288-42) displays the ordinary, single-pointed, crown, metrically resembling the teeth of the recent *P. tigris*. Meantime, this premolar is known to be somewhat more robust in *P. spelaea*.

One of two upper carnassial teeth P4 from Geographical Society Cave (ZIN 37288-114) is intact but heavily worn, especially in the area of the metastylar blade. Another tooth (ZIN 37288-4) is broken in the paracone area. Both fossil P4 from Geographical Society Cave are similar in maximum length to the teeth of recent *P. tigris altaica*, but smaller that the teeth of *P. spelaea* (Table 6). The tooth crown is wide owing to a pronounced inner shelf bearing a robust protocone. Both specimens exhibit a distinct preparastyle (Fig. 6A, B); the equal preparastyle is detected in half of specimens from the sample (n = 31) of recent *P. tigris altaica*. Additionally four P4 were recovered from Tigrovaya Cave (Fig. 6C–J). Their size and proportions resemble those of the specimens from Geographical Society Cave.

The ratio between the length of metastylar blade of P4 and the tooth greatest length varies in the examined sample of fossil *P. tigris* from 37.1% to 40.6% (mean 39.3%, n=5), which corresponds to the values of this index in recent *P. tigris altaica*: 34.7–43.3% (mean 39.7%, n=28). The recent *P. leo* have a smaller average index: 34.9–40.5% (mean 37.5%, n=14). The measured specimens of *P. spelaea* showed compara-

Table 4. Measurements (mm) of deciduous teeth in *Panthera*.

Localities	Museum number	LdC1	WdC1	Ldc1	Wdc1	Ld4	Lpard4	Wd4
P. tigris, Geographical Society Cave, Russia	ZIN 37288-6	9.3	6.7					
	ZIN 37288-1	8.8	6.4					
	ZIN 37288-67	7.7	6.0					
	ZIN 37288-2			11.3	5.4			
	ZIN 37288-69			10.2	–			
	ZIN 37288-71					18.5	7.8	7.2
P. tigris, recent, ♀	ZIN 36389	9.3	5.7	9.4	5.2	15.6	6.8	5.6
P. leo, recent	ZIN 31189	7.8	5.6	9.1	4.5	16.0	6.8	6.0

Table 5. Measurements (mm) of upper incisors I3 and upper canines C1 in *Panthera*.

Localities	Museum number	LI3	WI3	LC1	WC1
	P. tigris				
Geographical Society Cave, Russia	ZIN 37288-8	10.7	8.9		
	ZIN 37288-12	10.5	8.7		
	ZIN 37288-25	9.7	8.2		
	ZIN 37288-63	10.3	8.1		
	ZIN 37288-28			19.9	16.2
	ZIN 37288-29			21.6	16.0
	ZIN 37288-39			24.1	17.6
	ZIN 37288-61			20.0	16.6
Tigrovaya Cave	ZIN 37292-35			23.6	19.3
Letychaya Mysh Cave	ZIN n/n			21.5	17.0
P. tigris altaica, recent, ♀	ZIN 36369	10.5	9.1	21.0	16.1
	P. spelaea				
Geographical Society Cave, Russia	ZIN 37288-41			26.5	19.7
Zoolithen, Germany	NKHUB 48115-1			26.7	22.9
Köstritz, Germany	NKHUB 30064			26.3	18.4
Burgtonna, Germany	NKHUB 85			26.2	21.4
	NKHUB 83			26.4	19.6
Srbsko Chlum sluje Cave, Czech Republic	NHMP R4408			22.7	15.5
Berounca, Czech Republic	BM P363b			24.9	18.9
Duvanny Yar, Kolyma River, Russia	GMY 264			22.3	16.9
	P. leo				
Zoo, recent, ♀	ZIN 5726	10.6	9.8	19.8	14.4

tively shorter metastylar blades (29.5–38.7%, mean 35.6%, n=12); the maximum values of this index for the cave lion do not exeed mean values for the samples of fossil and recent tiger. Hence, the upper carnassial tooth of *P. tigris* shows a strengthening of trenchant function compared to *P. spelaea*.

For comparison, the cranial fragment (NKHUB 30002) from the Middle Pleistocene Trinil locality

Table 6. Measurements (mm) of upper check teeth in *Panthera*.

Localities	Museum number	LP2	WP2	LP4	LmtsP4	WP4
	P. tigris					
Geographical Society Cave, Russia	ZIN 37288-42	7.3	5.7			
	ZIN 37288-4			34.3	13.5	19.6
	ZIN 37288-114			32.6	12.1	19.0
Tigrovaya Cave	ZIN 37292-12			36.2	14.4	19.2
	ZIN 37292-13			35.9	14.2	19.0
	ZIN 37292-14			ca32.2	–	17.2
	ZIN 37292-25			34.7	14.1	18.5
†*Panthera tigris trinilensis*						
Trinil, Java, Indonesien	NKHUB 30002			32.8	12.1	17.6
P. tigris altaica, recent, ♀	ZIN 36369	7.5	5.3	33.1	12.4	15.8
	P. spelaea					
Zoolithen, Germany	NKHUB 48115-1			42.1	15.0	22.8
	NKHUB 30069			37.6	13.8	18.5
Peter Berg, Germany	NKHUB 29850			40.9	15.7	19.0
Srbsko Chlum sluje Cave, Czech Republic	NHMP R4408			34.3	12.1	17.5
Berounca, Czech Republic	BM P363b			37.4	13.1	20.5
Duvannyi Yar, Kolyma River, Russia	GMY 3190-1	6.2	6.1	37.1	13.1	19.1
	P. leo					
Zoo, recent, ♀	ZIN 5726	7.3	5.9	30.6	10.6	15.5

("*Pithecanthropus*-Schichten") in Java, Indonesia, which was originally described as *Feliopsis palaeojavanica* (Stremme 1911: 86; Taf. 16, Figs. 3, 4; Taf. 17, Fig. 1), was examined. Later, Königswald (1933) synonymized this taxon with the fossil subspecies *P. tigris trinilensis* (Dubois, 1908). The maxilla has P3–P4, alveoli of P2 and M1, and the alveolus of the canine with a broken root. The dimensions of P4 resemble those of specimens from Geographical Society Cave and Tigrovaya Cave (Table 6). The metastylar blade is short; the ratio between its length and the tooth greatest length (36.9%) is found to be near minimum values for *P. tigris* from Late Pleistocene of the Russian Far East. The anterior crown-margin is broken, which complicates the establishment of the preparastyle development (Fig 5C). It should be mentioned that *P. tigris trinilensis* had a long P3 (compared to P4). The ratio between the greatest length of P3 in this taxon and that of its P4 (70.1%) corresponds to the upper limit of variation of this index in recent *P. tigris altaica* (60.8–70.5%, averaging 64.8%, n=10).

Lower teeth occur more frequently than the upper teeth in the examined material. There are several isolated lower incisors resembling those of tiger and a single lower canine. The latter is large and may belong to a male (Table 7). The difference between the lower canines of *P. tigris* and *P. leo* is unclear.

There are several, mostly isolated, lower cheek teeth. The ratio between the width and length calculated for the premolar p3 varies in the sample from Tigrovaya Cave from 48.9% to 51.0% (mean 49.9%, n=6), which corresponds to males of recent *P. tigris altaica* (46.5–52.4%, mean 49.9%, n=5). Females of *P. t. altaica* are characterized by lower values of this index (43.8–50.0%, mean 47.5%, n=16). In contrast, values of this index for *P. spelaea* are larger (50.0–58.8%, mean 55.3%, n=11), i.e. the cave lion has a wider p3 (with regards to the tooth length) than *P. tigris*. Recent *P. leo* has an index of 46.7–57.8% (mean 52.2%, n=9).

The length of premolar p4 in the fossil *P. tigris* from Geographical Society Cave, Tigrovaya Cave,

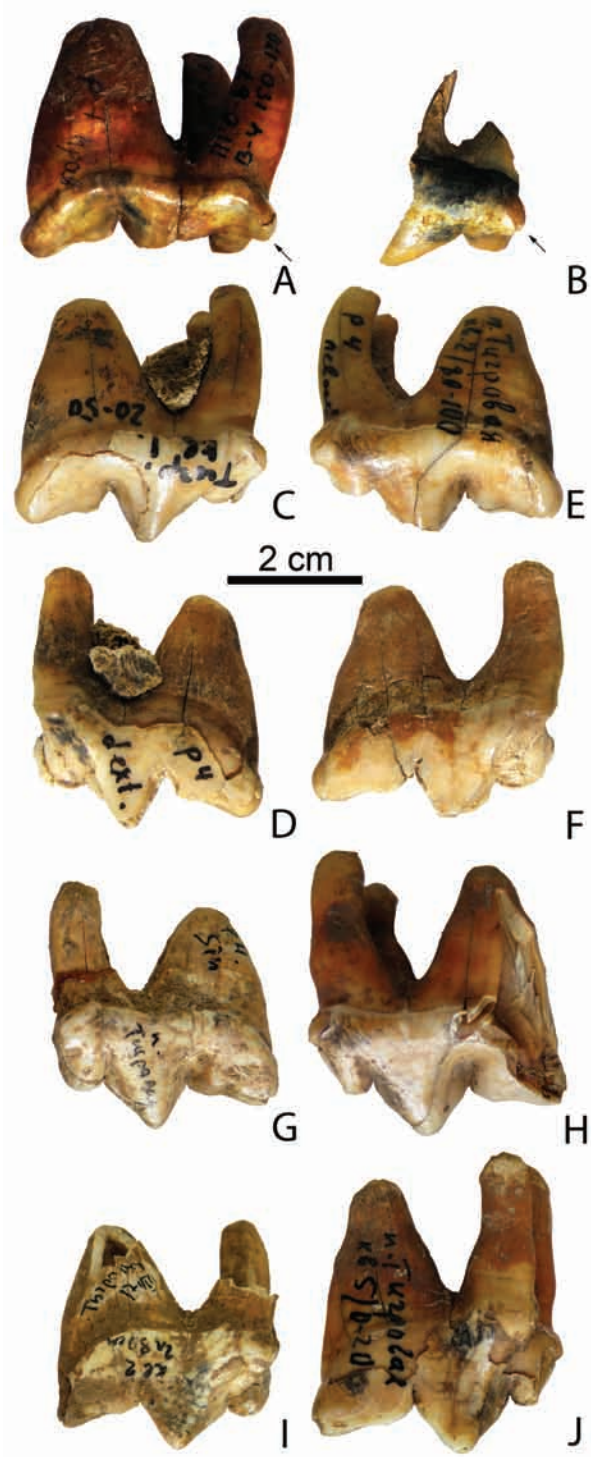

Fig. 6. *Panthera tigris*, Geographical Society Cave (A–B) and Tigrovaya Cave (C–J), upper carnassial teeth P4, buccal (A, B, C, E, H, I) and lingual (D, F, G, J) views; A – ZIN 37288-4, right, def.; B – ZIN 37288-114, right; C, D – ZIN 37292-25, right; E, F – ZIN 37292-12, left; G, I – ZIN 37292-14, left; H, J – ZIN 37292-13, left.

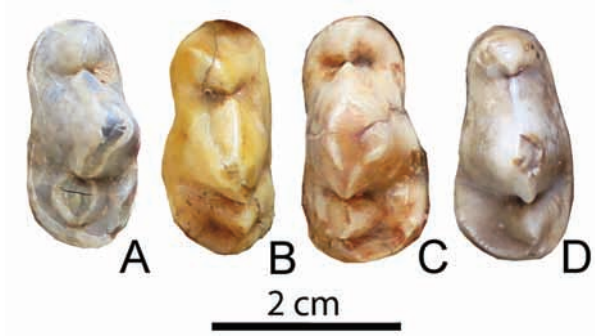

Fig. 7. *Panthera tigris* (A–B) and *P. spelaea* (C, D), lower premolar p4; occlusal view; A – ZIN 37288-23, left, Geographical Society Cave; B – ZIN 37295, right, Tigrovaya Cave; C – ZIN 34930-1, left, Geographical Society Cave; D – ZIN 24409-22, right, Binagady, Azerbaijan.

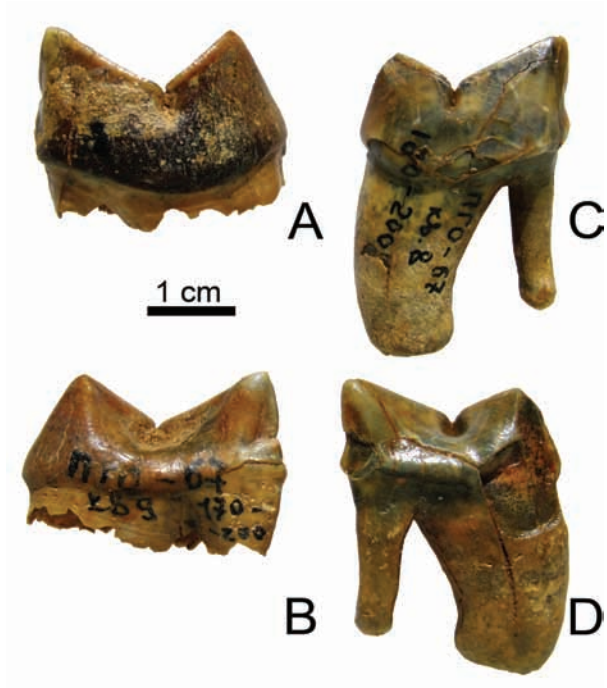

Fig. 8. *Panthera tigris*, Geographical Society Cave, lower carnassial teeth m1; buccal (A, C) and lingual (B, D) views; A, B – ZIN 34930-5, right; C, D – ZIN 34930-4, left.

and Malaya Pensau Cave is somewhat smaller compared to that of *P. spelaea*; however, the proportions of the tooth crown seem to be the same in both species (Table 8). The blade of the anterior cusp of p4 is turned lingually in recent *P. tigris*, whereas in *P. spelaea* and the *P. leo* it lies along the tooth axis or is slightly turned. The sample from Geographical Society Cave contains two specimens, which are similar

Table 7. Measurements (mm) of lower canine c1 in *Panthera*.

Localities	Museum number	Lc1	Wc1
	P. tigris		
Geographical Society Cave, Russia	ZIN 37288-33	24.0	18.3
	ZIN 37288-35	25.5	19.0
P. tigris altaica, recent, ♀	ZIN 36369	19.7	13.9
	P. spelaea		
Geographical Society Cave, Russia	ZIN 37930, right	27.8	18.5
	ZIN 37930, left	26.1	19.0
	ZIN 37933-4	23.9	19.4
Zoolithen, Germany	NKHUB 48115-2	26.1	17.3
	NKHUB 30071	29.6	18.8
	NKHUB 51130	26.2	18.9
Lauchstädt, Germany	NKHUB 30066	-	14.6
Hermannshöhle, Germany	NKHUB 14298	-	18.7
Burgtonna, Germany	NKHUB 81	23.8	18.7
Srbsko Chlum sluje Cave, Czech Republic	NHMP R4582	22.0	15.7
Svobodné Dvory Morávkova cihelna, Czech Republic	NHMP 26895	23.5	17.9
Praha-Podbaba, Czech Republik	NHMP R1	18.1	13.1
Berounca, Czech Republic	BM P363b	25.6	18.2
Liakhov Island, Arctic zone, Russia	ZIN 37909-1	25.1	18.8
	P. leo		
Zoo, recent, ♀	ZIN 5726	18.1	13.1

in this character to *P. tigris* (the other two teeth resemble *P. spelaea*) (Fig. 7A). The collection from Tigrovaya Cave and Malaya Pensau Cave included all premolars (n=7) corresponding to *P. tigris* (Fig. 7B). Two specimens of *P. spelaea vereshchagini* exhibit the anterior cusp of p4 lingually turned, as in *P. tigris*.

The greatest length of the lower carnassial tooth m1 varies from 26.3 mm to 28.9 mm (mean 27.59 mm, n=9) in fossil tiger from Geographical Society Cave, Tigrovaya Cave, Malaya Pensau, and Letuchaya Mysh Cave (Table 8). In recent *P. tigris altaica*, this tooth is markedly shortened with a greatest length of 23.2–26.2 mm in males (mean 24.83 mm, n=9) and 19.8–23.6 mm in females (mean 21.87 mm, n=17), i.e. male and female samples overlap slightly in this dimension. The m1 of *P. spelaea* on average markedly longer (25.6–31.7 mm, mean 29.15 mm, n=15).

A comparison of tiger m1 showed that it had a longer paraconid than that of the cave lion. Its length (measured from the crown anterior margin to the carnassial notch) in Late Pleistocene *P. tigris* is more than half the length of the tooth crown: the ratio between the paraconid length and the tooth greatest length is 53.3–58.6% (mean 55.6%, n=10). In *P. spelaea*, the values of this index are somewhat smaller (45.2–55.6%, mean 51.8%, n=15).

On average the fossil tiger is characterized by a slightly wider m1 (with regards to the tooth greatest length) than in recent *P. tigris altaica*. The ratio between the width and length of this tooth varies in the fossil tiger from 45.9% to 51.8% (mean 49.2%, n=8), whereas in recent *P. tigris altaica* (males and females) it is 42.1–50.2% (mean 46.5%, n=21).

Nearly all m1 specimens (nine out of ten) in the fossil tiger show a reduced metaconid in the shape of a small cuspid placed at the base of the posterior margin of the protoconid (Figs. 8, 9). The metaconid was found in only half of the specimens from the examined sample (n=20) of the *P. tigris altaica*.

Vereshchagin (1971) noted that the divergence of paraconid and protoconid cones had developed in the evolution of felids, accompanied by the straightening

Table 8. Measurements (mm) of lower cheek teeth of Late Pleistocene *Panthera*.

Localities	Museum number	Lp3	Wp3	Lp4	Wp4	Lm1	Lparm1	Wm1
		P. tigris						
Geographical Society Cave, Russia	ZIN 37930-2					24.6	13.5	12.4
	ZIN 34930-4					–	–	13.0
	ZIN 34930-5					27.5	15.3	13.4
	ZIN 37288-9			25.0	11.9			
	ZIN 37288-23			24.8	12.2			
	ZIN 37288-16					–	–	13.9
	ZIN 37288-19					–	14.5	12.9
Tigrovaya Cave	ZIN 37295			26.4	13.2	28.6	16.5	13.9
	ZIN 37292-4	19.8	10.0	27.0	14.0			
	ZIN 37292-5	19.0	9.3					
	ZIN 37292-19	19.5	9.6					
	ZIN 37292-27	17.2	7.0					
	ZIN 37292-28	15.6	7.0					
	ZIN 37292-29	19.0	9.7					
	ZIN 37292-2			23.7	12.4			
	ZIN 37292-10			25.2	13.1			
	ZIN 37292-20			26.9	12.7			
	ZIN 37292-22			24.6	12.6			
	ZIN 37292-23			25.8	12.7			
	ZIN 37292-1			25.7	12.2	27.8	16.3	14.0
	ZIN 37292-16					28.9	15.9	14.5
	ZIN 37292-17					28.0	16.0	14.5
Letuchaya Mysh Cave	ZIN 37292-8					26.5	14.9	12.8
Malaya Pensau Cave	ZIN 37293					28.1	14.4	13.4
	ZIN 37294			23.7	11.8	28.3	15.1	13.0
	ZIN 37288-10					–	14.0	13.0
P. tigris altaica, recent, ♀	ZIN 36369	15.0	7.3	21.5	9.8	22.0	10.9	10.5
		P. spelaea						
Geographical Society Cave, Russia	ZIN 37930	18.4	10.4	27.8	13.1			
	ZIN 37931	15.6	8.3	23.6	–	26.3	14.3	13.6
	ZIN 37932					27.9	15.7	15.2
Zuzelga, Ural, Russia	IEPA 394-2	16.4	9.0	26.0	12.0	28.5	14.6	13.4
Zapovednaya, Ural, Russia	IEPA 639-15448	19.2	11.3	28.3	13.9	30.8	16.2	15.0
Secrets Cave, Ural, Russia	IEPA 810-7466	16.1	9.1	26.0	12.4	25.6	14.0	13.4
Nizhniya Tavda 1, Ural, Russia	IEPA 178-872			27.8	12.8	30.8	14.8	14.4
Zoolithen, Germany	NKHUB 48115-2	18.3	10.2	26.3	13.2	30.3	13.7	14.7
	NKHUB 30073	20.8	11.5	29.9	14.7	31.7	15.9	15.9
Lauchstädt, Germany	NKHUB 30066	17.0	9.5	25.4	12.5	27.5	13.5	13.8

Table 8. *Continued*.

Localities	Museum number	Lp3	Wp3	Lp4	Wp4	Lm1	Lparm1	Wm1
Hermannshöhle, Germany	NKHUB 14298	19.0	9.6	27.6	13.4			
Burgtonna, Germany	NKHUB 81			26.3	13.7	30.6	16.3	14.9
Phoeben, Germany	NKHUB 30067	15.4	8.8	24.3	12.0			
Roter Berg, Germany	NKHUB 30061					31.3	17.4	15.4
Dechenhöhle, Germany	NKHUB 106					28.5	14.7	14.5
Srbsko Chlum-Komín Cave, Czech Republic	NHMP R4582	15.7	8.9	24.2	11.6	27.6	15.1	14.1
Svobodné Dvory Morávkova cihelna, Czech Republic	NHMP 26895	17.4	9.9	25.3	13.4	29.4	15.7	13.5
Praha-Podbaba, Czech Republik	NHMP R1	15.2	7.6	23.5	10.9	26.1	13.2	12.4
Berounca, Czech Republic	BM P363b			27.3	13.2	29.9	16.2	14.1
Berezovka River	ZIN 329405			25.3	12.7	28.6	15.6	14.4
Liakhov Island, Arctic zone, Russia	ZIN 37909-2			27.7	12.7			

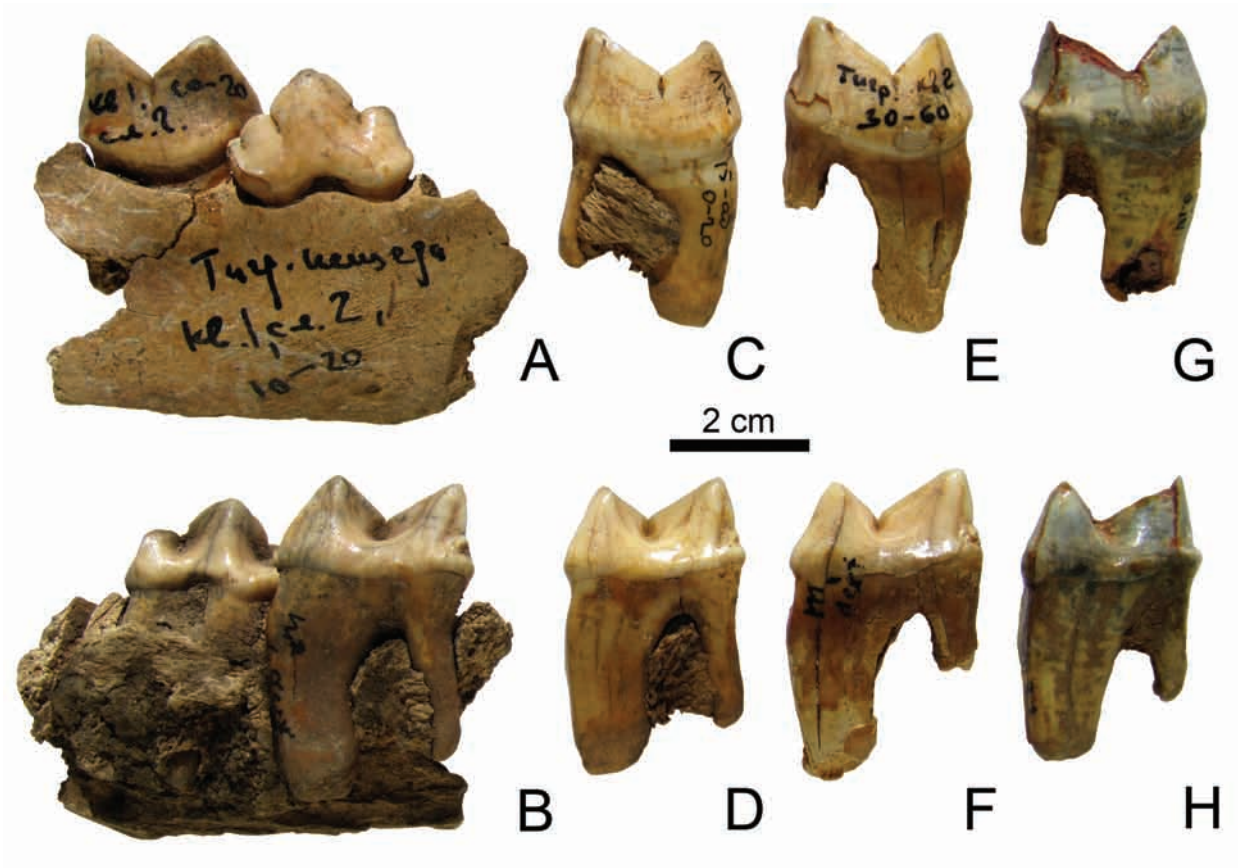

Fig. 9. *Panthera tigris*, Tigrovaya Cave, lower carnassial teeth, buccal (A, C, E, G) and lingual (B, D, F, H) views; A, B – ZIN 37292-1, p4–m1, right; C, D – ZIN 37292-8, m1, right; E, F – ZIN 37292-17, m1, right; G, H – ZIN 37292-15, m1, right.

and more parallel positioning of their outer margins, as previously noticed by Freudenberg (1914). According to Vereshchagin's calculations (1971: 132), the ratio between the distance connecting the paraconid and protoconid apices and the greatest length of m1, in average, corresponds to 70.9% (n=10) in fossil *P. tigris* from the caves from Russian Far East and 75.3% (n=10) in recent *P. tigris*.

Thus the lower carnassial tooth m1 of the fossil tiger is more primitively shaped compared to that of the recent *P. tigris altaica*. The recent tiger has a narrower m1, its metaconid is less often developed, and there is more pronounced divergence between the paraconid and protoconid cones, which indicates the strengthening of trenchant function in the dentition of the recent tiger and testifies to a rather fast rate of evolution in *P. tigris* from the Late Pleistocene to the present time (Vereshchagin 1971: 136). However, a different explanation may be hypothesized: in which the Pleistocene populations were replaced by populations with a more progressive dentition, as a result of the tiger migration to southern regions of the Russian Far East in the Holocene.

The comparison of dental morphology between *P. tigris* and *P. spelaea* shows that the teeth of *P. tigris*, a solitary hunter, are characterized by a more pronounced trenchant function (carnivorous specialization) than the teeth of *P. spelaea* which lived in groups (prides) similar to the recent lion.

Fore limb bones. The humerus is represented by distal fragments. The size of the examined humeri seems smaller than that of *P. spelaea*. The tuberosity on the medial side of the epicondylus medialis gradually declines distally, as in *P. tigris* (whereas in recent *P. leo* this tuberosity is steeply descending distally, see Gromova 1950).

There are several large fragments of ulna, which allows them to be reliably referred to *P. tigris*. The volar margin is convex (it is concave in *P. leo*), the lateral surface of the upper part at the level of the incisura semilunaris is concave, shaped as a groove, and bordered along the outer margin by a longitudinal ridge (*P. leo* has the flat surface, which does not have this longitudinal ridge); the anterior portion of the tuberosity olecrani is markedly distanced from the incisura semilunaris (these regions are closer in *P. leo*) (Gromova 1950, Vangengeim 1961). The parameters of the fossil fragmentary ulnas do not exceed the size of the ulna in recent *P. tigris*; in *P. spelaea* and *P. leo* this bone is noticeably larger (Table 9).

The collection from Geographical Society Cave includes a single, intact, radius (ZIN 37288-50, depth 160–180 cm). In its greatest length, it is similar to the radius of *Felis* cf. *tigris* from Zhoukoudian 1 in China (Pei 1934). The tuberositas radii of ZIN 37288-50 steeply declines distally, in a similar way to *P. tigris* (in *P. leo* it descends gradually). The fossil radius can be referred to a female from its size.

The metacarpal 1 (mc1) of felids is known to be markedly reduced in size (Fig. 10A, B). Its dimensions overlap *P. spelaea* and recent *P. leo* and *P. tigris* (Table 10, see also Baryshnikov 2011). Morphological differences between these bones are unclear in *P. leo* and *P. tigris*. The fossil specimen (ZIN 37288-43) is minute; it is very much smaller than the examined specimens of *P. tigris*, *P. spelaea*, and *P. leo*.

The metacarpals 2 (mc2) from Geographical Society Cave (Fig. 10C, D) are small in comparison with *P. spelaea*, displaying no metric difference from recent *P. tigris* (Table 10). Discriminant Analysis performed on the basis of 6 measurements separates the fossil specimens from *P. spelaea* and *P. leo*, placing them close to recent *P. tigris* (Fig. 11). Within the scatterplot of canonical scores, the examined samples predominantly group by Root 1 (measurements of *Bp* and *GL*); the divergence by Root 2 (*SD*) is less pronounced. The proximal articular facet of mc2, which contacts the os multangulum minus, is more markedly narrowed in the volar direction in *P. leo* than in *P. tigris*; the specimens from Geographical Society Cave resemble *P. tigris* in this character.

The fossil metacarpals 3 (mc3; Fig. 10E, F) are markedly smaller than those of *P. spelaea*, corresponding to recent *P. tigris* (Table 10). The metacarpal of *P. leo* differs from that of *P. tigris* by having a wider proximal articular facet whose volar process forms a distinct, rather small ridge at its lateral margin; whereas this ridge is poorly marked in *P. tigris*. Six specimens from Geographical Society Cave reveal no this ridge; however, two other specimens display poorly developed ridges. In *P. spelaea vereshchagini* from the Yana River in Yakutia (ZIN 30884) this bone is characterized by the distinctive ridge, similarly to *P. leo*.

The dimensions of the metacarpal 4 (mc4; Fig. 10G, H) from Geographical Society Cave correspond to those of recent *P. tigris* and surrender the bone measurements of *P. spelaea* (Table 10). The proximal articular facet of mc4 of the recent *P. leo* reveals the well-developed ridge separating the area,

Table 9. Measurements (mm) of hind limb bones in *Panthera*.

Locality	Museum number	GL	Bp	SD	Bd	Dp	SDO	DPA	BPC
		Humerus							
		P. tigris							
Geographical Society Cave, Russia	ZIN 37288-85				73.3				
	ZIN 37288-86			25.2	69.7				
Turkestan, Central Asia, recent	ZIN 14997	333.3	76.5	28.9	87.1	90.3			
		P. spelaea							
Pobeda Cave, Ural, Russia	IEPA n/n			29.4	86.8				
	IEPA n/n	362.0	–	34.3	99.1	109.3			
Zoolithen, Germany	NKHUB 1955	350.0	–	36.7	95.3	107.5			
	NKHUB 1956	340.0	88.1	33.9	92.4	107.2			
	NKHUB 1957	335.0	86.7	38.5	93.6	108.6			
Hermannshöhle, Germany	NKHUB 14336	350.0	85.2	34.2	94.7	106.9			
	NKHUB 14337	345.0	82.5	34.6	93.8	110.1			
Srbsko Chlum Komin Cave, Czech Republic	NHMP R4417	317.0	–	29.0	85.2	93.7			
Duvannyi Yar, Kolyma River, Russia	MMY n/n	320.8	64.7	27.0	83.9	93.7			
		P. leo							
Zoo, recent	ZIN 4047	330.5	86.2	28.6	91.5	100.0			
		Ulna							
		P. tigris							
Geographical Society Cave, Russia	ZIN 37288-49								42.9
	ZIN 37288-75								43.9
	ZIN 37288-76						38.3	50.4	36.9
	ZIN 37288-79								39.1
	ZIN 37288-132								ca36.5
Turkestan, Central Asia, recent	ZIN 14997	347.8					43.8	51.8	45.5
		P. spelaea							
Abatskoe, Western Siberia, Russia	IEPA 1474-47						50.7	65.0	49.8
Secrets Cave, Ural, Russia	IEPA 810-62	399.0						72.7	51.8
Sundwig, Germany	NKHUB 48284	380.0					56.7	72.6	52.6
Niederlehme, Germany	NKHUB 30090	345.0					50.3	62.2	45.9
Srbsko Chlum Komin Cave, Czech Republic	NHMP R4418	348.0						66.8	50.9
	NHMP R4419	346.0						68.2	49.7
		P. leo							
Zoo, recent	ZIN 4047	358.8					53.9	64.4	51.5
		Radius							
		P. tigris							
Geographical Society Cave, Russia	ZIN 37288-50	256.1	32.3	23.8	48.6				
	ZIN 37288-78				51.8				

Table 9. *Continued.*

Locality	Museum number	GL	Bp	SD	Bd	Dp	SDO	DPA	BPC
	ZIN 37288-80		31.9						
Turkestan, Central Asia, recent	ZIN 14997	299.1	37.1	29.0	54.2				
		P. spelaea							
Kholodnyi Grotto, Ural, Russia	IEPA 816-169	306.0	44.0	30.5	63.5				
Cheremukhovo 1 Cave, Ural, Russia	IEPA 977-2160	283.2	42.8	29.4	62.5				
Irtysh River, Western Siberia, Russia	IEPA 915-316	285.8	38.5	31.5	59.8				
Zoolithen, Germany	NKHUB 2246	355.0	56.0	31.3	68.5				
Hermannshöhle, Germany	NKHUB 14332	330.0	45.1	36.8	69.3				
Niederlehme, Germany	NKHUB 30091	320.0	48.4	36.2	70.7				
Türmitz, Germany	NKHUB 30092	305.0	47.8	35.1	69.7				
Senzig, Germany	NKHUB 30093	305.0	46.7	33.1	68.5				
Lauchstädt, Germany	NKHUB 30096	280.0	41.6	28.5	55.4				
Seddin, Germany	NKHUB 40	325.0	48.9	38.1	65.6				
Srbsko Chlum Komin Cave, Czech Republic	NHMP R4420	286.6	40.0	29.1	62.6				
	NHMP R5386	291.4	41.1	27.7	62.5				
		P. leo							
Zoo, recent	ZIN 4047	301.8	46.2	26.9	64.2				

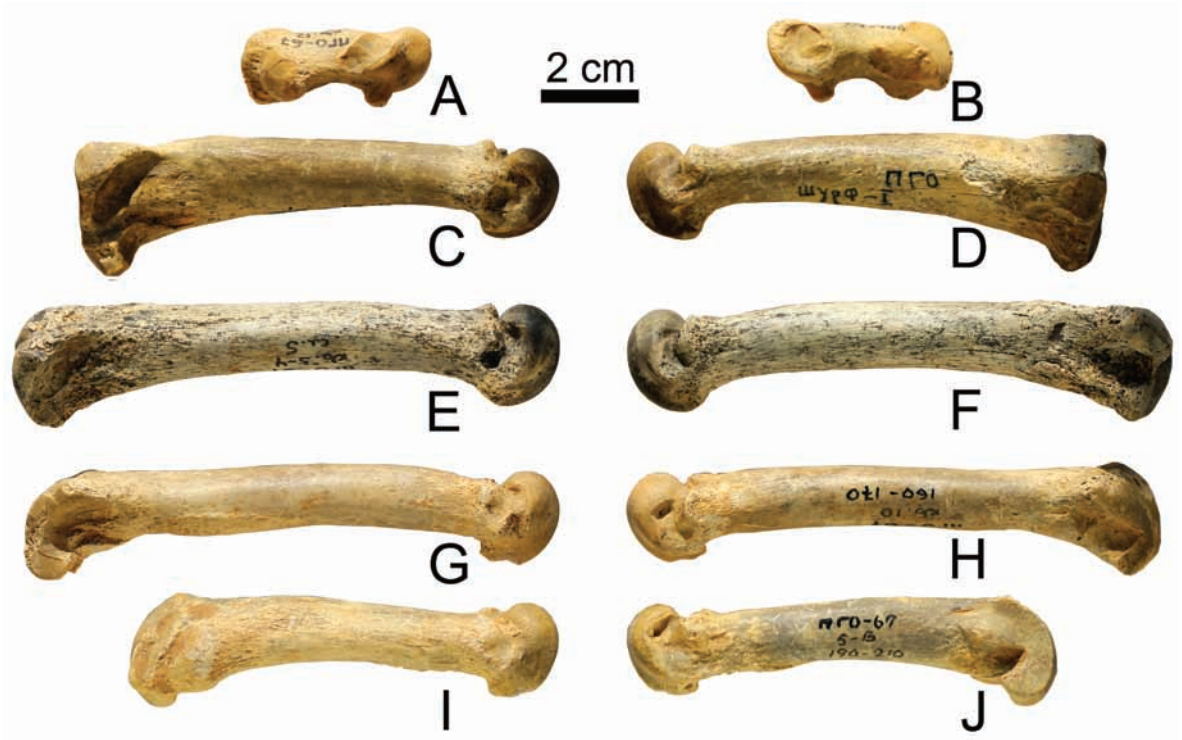

Fig. 10. *Panthera tigris*, Geographical Society Cave, carpals (lateral (A, D, F, I) and medial (B, C, E, J) views; A, B – mc1 (ZIN 37288-43), left; C, D – mc2 (ZIN 37288-143), left; E, F – mc3 (ZIN 37288-111), left; G, H – mc4 (ZIN 37288-45), left; I, J, – mc5 (ZIN 37288-47), right.

Table 10. Measurements (mm) of metacarpal bones in *Panthera*.

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd
	Mc 1						
	P. tigris						
Geographical Society Cave, Russia	ZIN 37288-43	35.0	16.8	14.4	13.1	14.3	14.1
P. t. virgata, Turkestan, recent	ZIN 14997	41.5	24.1	18.9	16.8	18.9	17.7
P. t. sumatrana, zoo, recent, ♂	ZIN 30964	40.3	22.5	17.8	14.7	17.7	17.7
Zoo, recent	ZIN 1893	40.6	23.2	19.4	14.6	18.2	17.3
	P. spelaea						
Hermannshöhle, Germany	NKHUB 14321	47.9	25.9	20.4	16.8	20.2	18.8
	P. leo						
Zoo, recent, ♂	ZIN 30373	45.1	20.5	15.1	13.5	15.7	14.2
Zoo, recent	ZIN 4047	42.7	23.1	17.6	16.5	18.6	18.4
	Mc 2						
	P. tigris						
Geographical Society Cave, Russia	ZIN 37288-143	95.2	19.7	26.4	12.6	19.7	19.8
	ZIN 37288-144	94.9	19.7	26.1	12.5	19.7	20.0
	ZIN 37288-145	99.5	20.6	26.4	12.7	19.5	–
	ZIN 37288-146	98.9	21.0	26.1	12.3	19.7	18.7
P. t. virgata, Turkestan, recent	ZIN 14997	101.4	22.6	28.6	13.8	22.6	21.6
P. t. sumatrana, zoo, recent, ♂	ZIN 30964	95.2	21.4	28.5	13.1	21.3	21.2
Zoo, recent	ZIN 1893	99.2	22.2	27.7	13.6	22.2	20.8
	P. spelaea						
Pobeda Cave, Ural, Russia	IEPA 467-n/n	108.5	22.7	31.3	15.7	22.9	22.1
Cheremukhovo 1 Cave, Ural, Russia	IEPA 977-2854	108.6	24.6	34.0	16.1	25.1	24.4
Dechenhöhle, Germany	NKHUB 30146	102.4	21.3	30.6	15.9	21.0	20.7
Oderberg-Bralitz, Germany	NKHUB 30144	106.3	20.9	28.4	14.8	21.0	–
Hermannshöhle, Germany	NKHUB 14317	115.1	26.5	33.4	17.5	25.8	23.3
	P. leo						
Zoo, recent, ♂	ZIN 30373	111.5	22.5	29.4	12.6	22.2	20.5
Zoo, recent	ZIN 4047	106.7	24.3	31.7	13.9	23.3	23.1
	Mc 3						
	P. tigris						
Geographical Society Cave, Russia	ZIN 37288-44	106.1	22.1	24.1	13.9	21.5	18.6
	ZIN 37288-102	107.1	23.6	24.2	13.6	21.7	19.0
	ZIN 37288-109	–	24.3	25.5	15.8	–	–
	ZIN 37288-110	–	21.5	24.4	14.0	–	–
	ZIN 37288-111	107.7	21.7	23.9	14.7	20.8	20.3
	ZIN 37288-112	111.7	21.3	23.8	13.2	20.5	18.9
	ZIN 37288-113	–	24.0	23.4	–	–	–
P. t. virgata, Turkestan, recent	ZIN 14997	124.5	24.1	28.7	14.9	24.2	20.3

Table 10. *Continued*.

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd
P. t. sumatrana, zoo, recent, ♂	ZIN 30964	109.8	27.5	27.6	14.2	23.6	20.5
Zoo, recent	ZIN 1893	113.2	27.4	29.5	12.4	23.8	19.9
	P. spelaea						
Pobeda Cave, Ural, Russia	IEPA 467-n/n	115.1	25.2	28.7	–	23.4	20.2
Zapovednaya Cave, Ural, Russia	IEPA 639-9175	130.0	30.0	31.8	19.1	28.4	25.3
Zoolithen, Germany	NKHUB 30139	123.0	29.8	32.0	18.4	23.7	24.0
Senzig, Germany	NKHUB 30135	121.9	31.7	30.9	16.0	24.8	22.2
Kauffung, Poland	NKHUB 30145	138.0	29.3	30.9	19.7	26.1	ca21.5
Yana River. Russia	ZIN 30884	111.2	28.6	26.4	15.7	22.3	21.2
	P. leo						
Zoo, recent, ♂	ZIN 30373	124.6	25.8	28.2	14.7	24.0	20.3
Zoo, recent	ZIN 4047	121.6	27.7	32.4	15.5	25.5	22.7
	Mc 4						
	P. tigris						
Geographical Society Cave, Russia	ZIN 37288-45	105.5	18.3	20.7	12.3	18.3	18.5
	ZIN 37288-99	–	20.7	25.1	13.9	–	–
	ZIN 37288-101	–	18.4	22.2	–	–	–
P. t. virgata, Turkestan, recent	ZIN 14997	107.1	19.8	24.5	13.9	21.5	20.4
P. t. sumatrana, zoo, recent, ♂	ZIN 30964	105.1	21.8	23.9	14.1	21.4	20.5
Zoo, recent	ZIN 1893	107.0	20.5	24.5	12.2	20.7	19.6
	P. spelaea						
Achinsk, Western Siberia, Russia	ZIN 17286	123.1	23.7	30.6	16.1	23.0	24.1
Ignatievskaya Cave, Ural, Russia	IEPA 253-1065	128.5	26.4	35.6	17.2	24.2	20.8
Pobeda Cave, Ural, Russia	IEPA 467-n/n	134.2	26.6	33.9	18.7	28.1	26.6
Zoolithen, Germany	NKHUB 30138	129.5	24.8	32.1	16.7	24.5	24.3
Hermannshöhle, Germany	NKHUB 14320	120.3	24.1	28.7	16.2	24.3	23.8
Christburg, Poland	NKHUB 9443	134.6	27.4	30.6	20.8	28.0	24.6
Srbsko Chlum Komin Cave, Czech Republic	NHMP R4535	109.4	22.8	28.6	14.2	20.6	21.4
	NHMP R5148	111.4	27.7	26.1	15.0	22.2	21.5
	NHMP R5149	108.6	22.3	27.5	14.5	20.7	21.2
	P. leo						
Zoo, recent, ♂	ZIN 30373	119.4	20.6	26.2	14.3	22.3	20.7
Zoo, recent	ZIN 4047	118.3	24.3	27.3	15.0	23.9	23.2
	Mc 5						
	P. tigris						
Geographical Society Cave, Russia	ZIN 37288-47	85.1	20.0	22.7	12.0	19.4	18.7
	ZIN 37288-107	–	21.9	23.9	12.7	–	–
	ZIN 37288-108	–	20.3	21.1	11.6	–	–
	ZIN 37288-131	–	19.8	20.9	11.7	–	–
P. t. virgata, Turkestan, recent	ZIN 14997	86.7	21.5	24.4	12.4	19.9	20.3

Table 10. *Continued*.

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd
P. t. sumatrana, Zoo, recent, ♂	ZIN 30964	83.7	22.1	22.5	12.4	20.7	20.5
Zoo, recent	ZIN 1893	85.3	23.8	24.3	12.1	20.0	19.5
	P. spelaea						
Pobeda Cave, Ural, Russia	IEPA 467-3150	92.5	23.9	25.2	14.1	20.6	–
	IEPA 467-n/n	98.8	26.2	28.9	16.9	23.5	21.9
Hermannshöhle, Germany	NKHUB 14318	105.7	28.7	30.4	17.7	24.3	23.1
	NKHUB 14319	104.5	26.5	31.2	17.1	24.2	23.1
Srbsko Chlum Komin Cave, Czech Republic	NHMP R4536	89.6	25.6	26.6	14.3	20.9	20.7
	NHMP R5150	89.0	24.9	26.0	12.8	20.3	19.2
	P. leo						
Zoo, recent, ♂	ZIN 30373	99.8	25.3	24.4	13.1	20.8	19.8
Zoo, recent	ZIN 4047	96.2	28.9	28.5	15.4	23.1	22.1

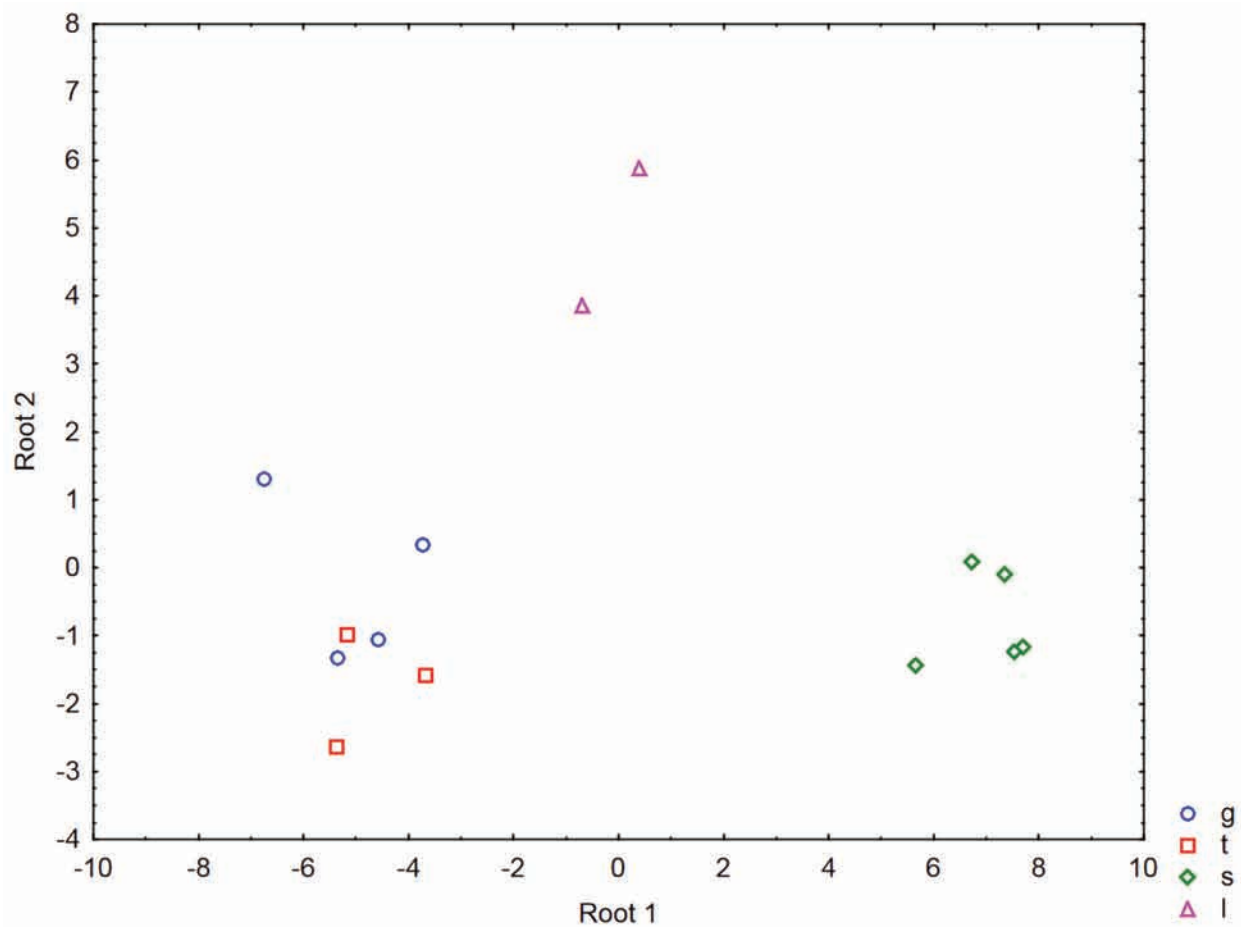

Fig. 11. Scatterplot of canonical scores for panther metacarpus 2 (mc2); g – fossil *Panthera tigris*, Geographical Society Cave, l – *P. leo*, s – *P. spelaea*, t – recent *P. tigris*.

which is adjacent to os hamatum, from the facet portion, which is articulated with mc3. The specimens from Geographical Society Cave referred to *P. tigris* display the weakly developed ridge or it is indistinct.

The incomplete fossil metacarpals 5 (mc5) coincide in size and proportions with *P. tigris* (Fig. 10I, J). The metacarpals are markedly small compared with those of *P. spelaea* and recent *P. leo* (Table 10). However, no difference has been detected between the mc5 of *P. tigris* and that of *P. leo*.

Hind limb bones. Tibiae are represented only by distal fragments, and the distal parts of these bones poorly distinguishable between *P. tigris* and *P. leo*. Gromova (1950) noted that *P. leo* is characterized by a concave, groove-like, shelf on the volar margin of the distal trochlea, which extends along the volar surface; in *P. tigris*, this shelf is flat or slightly concave. The examined tibiae remains from Geographical Society Cave are similar to *P. tigris* in this character.

There are two right and four left fossil heel bones (os calcaneus). One of them (ZIN 37288-58) which is larger could belong to a male; other specimens should be referred to females. All bones, with exception of the largest, are smaller than the same bones of *P. spelaea*, corresponding in size to os calcaneus of recent *P. tigris* (Table 11). In addition, the outer shelf of its distal part is not restricted ventrally by a depression (in *P. leo* the shelf has this depression); the distal part of the heel bone is subtriangular in the outline and its width exceeds its thickness (it is rounded in *P. leo* with both dimensions nearly equivalent) (Gromova 1960; Vangengeim 1961).

Only two specimens from four astragali (os talus) are intact. ZIN 37288-56 is markedly larger than ZIN 37288-55; the former may be referred to a male and the latter to a female. The parameters of astragali from Geographical Society Cave are markedly smaller than those of *P. spelaea* (Table 11) resembling *Felis* cf. *tigris* from Zhoukoudian 1 in China (Pei 1934). The difference between the tiger astragalus and that of the lion is not clear. Probably, the talus head is narrower in the tiger (the ratio between the width and length of the head is 70–75%) whereas in the lion it is 78–82% (Gromova 1960). The examined specimens had a ratio of 76–79% (n=3), which is similar to that of *P. tigris*. In addition the distal end of tibial trochlea exhibits a small elevation, as in *P. tigris* (no elevation is observed on this part of the trochlea in *P. leo*).

The material studied comprises one intact specimen and one fragment of metatarsal 2 (mt2) (Fig. 12A, B). These are small, corresponding to those of recent *P. tigris* (Table 12). The recent *P. leo* has the proximal articular facet abruptly ascending at the volar margin, forming a distinctive tuberosity (which is well observed in lateral view); this feature is only inconspicuously marked in *P. tigris*. The shape of the proximal facet in the material from Geographical Society Cave resembles that of *P. tigris*. Both bones of *P. spelaea vereshchagini* from Eastern Siberia (ZIN 4224, 21846) examined for comparative purposes resemble recent *P. leo*.

The measurements of fossil metatarsals 3 (mt3; Fig. 12, C, D) do not exceed those of recent *P. tigris* (Table 12). In mt3 there is a difference between *P. tigris* and *P. leo* in the shape of the proximal articular facet adjoining to os cuneiforme 3. Its volar part is widened in *P. tigris* and separated from the dorsal part by a distinct compression. In *P. leo*, the volar part of the facet is narrower and poorly separated from the dorsal part. The shape of specimens from Geographical Society Cave resembles *P. tigris*. The size and proportions of mt3 of *P. spelaea vereshchagini* resemble those of *P. tigris*.

The dimensions of metatarsals 4 (mt4) from Geographical Society Cave do not exceed the size of this bone in recent *P. tigris*, excepting ZIN 37288-51 which is referred to *P. spelaea* (Table 12). The proximal facet articulated with os cuboideum is more elongated in the dorsal-volar direction in *P. spelaea* and in recent *P. leo* in comparison with *P. tigris*. In the ratio of width to thickness of the proximal margin, these bones from Geographical Society Cave are similar to *P. tigris* and are clearly distinguishable from *P. leo* and *P. spelaea* (Fig. 13). The articular facet of mt4 adjoining to os cuboideum is more pronouncedly separated in *P. leo* from the proximal facet articulated with mt3, in comparison with *P. tigris* whose facets on mt4 frequently contact. In this character, the specimens from Geographical Society Cave, and the bone of *P. spelaea vereshchagini* from the Arctic coast (Rebrov River, ZIN 35047), resemble *P. tigris*.

In summary, the size of metacarpals and metatarsals of the fossil tiger do not exceed those of males of the recent tiger; although the tooth dimensions (especially, length of m1) of the latter species are smaller.

Thus, the shape and size of postcranial bones of the large felid from Geographical Society Cave correspond to those of *P. tigris*. However, several features are also characteristic of *P. spelaea vereshchagini*,

Table 11. Measurements (mm) of hind limb bones in *Panthera*.

Locality	Museum number	GL	Bp	SD	Bd	GB
	Patella					
	P. tigris					
Turkestan, Central Asia, recent	ZIN 14997	50.8				34.9
Zoo, recent	ZIN 1893	53.8				34.9
	P. spelaea					
Geographical Society Cave, Russia	ZIN 37933-3	57.8				39.1
Zoolithen, Germany	NKHUB 3844	57.2				35.2
	NKHUB 3845	59.4				40.6
Srbsko Chlum Komin Cave, Czech Republic	NHMP R4533	59.0				41.1
	NHMP R4602	58.7				41.4
	P. leo					
Zoo, recent	ZIN 4047	55.9				42.7
	Tibia					
	P. tigris					
Geographical Society Cave, Russia	ZIN 37288-81			26.5		
	ZIN 37288-82			23.5	ca45	
	ZIN 37288-83				48.4	
Turkestan, Central Asia, recent	ZIN 14997	322.7	79.8	29.3	57.0	
	P. spelaea					
Irtysh River, Western Siberia, Russia	IEPA 915-124			25.8	58.5	
Pobeda Cave, Ural, Russia	IEPA 467-n/n	333.0	75.7	30.1	58.7	
Zoolithen, Germany	NKHUB 1940	360.0	95.2	36.4	69.2	
	NKHUB 1942	355.0	95.7	36.8	ca65	
	NKHUB 1943	345.0	95.9	33.7	67.4	
	NKHUB 1944	350.0	96.7	35.5	70.8	
	NKHUB 1945	350.0	97.4	34.0	67.0	
	NKHUB 1946	345.0	94.7	33.3	66.8	
Niederlehme, Germany	NKHUB 1941	350.0	87.3	30.6	64.0	
Kleinbesten, Germany	NKHUB 51262	325.0	86.7	29.6	63.7	
Srbsko Chlum Komin Cave, Czech Republic	NHMP R4527	313.0	84.1	29.0	61.0	
	NHMP R4528	312.0	83.1	29.3	63.9	
	P. leo					
Zoo, recent	ZIN 4047	318.7	86.9	28.7	66.3	
	Calcaneum					
	P. tigris					
Geographical Society Cave, Russia	ZIN 37288-58	114.9				51.0
	ZIN 37288-59	107.3				48.9
	ZIN 37288-60	100.4				46.7
	ZIN 37288-88	103.9				48.7

Table 11. *Continued.*

Locality	Museum number	GL	Bp	SD	Bd	GB
	ZIN 37288-89					48.0
Turkestan, Central Asia, recent	ZIN 14997	106.5				46.5
Zoo, recent	ZIN 1893	104.8				45.4
	P. spelaea					
Pobeda Cave, Ural, Russia	IEPA 467-n/n	120.7				54.9
	IEPA 467-3791	114.4				48.7
	IEPA 467-5654	126.9				58.8
Zoolithen, Germany	NKHUB 30112a	134.0				60.8
	NKHUB 30112b	134.9				62.2
Thiede, Germany	NKHUB 30105	112.4				50.7
Srbsko Chlum Komin Cave, Czech Republic	NHMP R4530	113.2				47.7
	P. leo					
Zoo, recent, ♂	ZIN 30373	116.8				51.8
Zoo, recent	ZIN 4047	119.3				56.5
	Talus					
	P. tigris					
Geographical Society Cave, Russia	ZIN 37288-55	50.6				42.9
	ZIN 37288-56	56.5				47.1
	ZIN 37288-57	49.7				ca40
	ZIN 37288-128	51.6				–
Turkestan, Central Asia, recent	ZIN 14997	56.3				45.2
Zoo, recent	ZIN 1893	57.5				51.8
	P. spelaea					
Pobeda Cave, Ural, Russia	IEPA 4673148	62.1				49.5
Zoolithen, Germany	NKHUB 30116	68.6				58.0
Dechenhöhle, Germany	NKHUB 30111	64.3				54.8
Srbsko Chlum Komin Cave, Czech Republic	NHMP R4531	57.6				47.9
	NHMP R4914	57.4				48.1
	P. leo					
Zoo, recent, ♂	ZIN 30373	52.3				46.1
Zoo, recent	ZIN 4047	63.7				53.5

which creates difficulties for the accurate attribution of the fossil collection.

Discussion. The present study demonstrates that remains of large-felids from Geographical Society Cave predominantly belong to *P. tigris*. In the Primorskii Territory, this big cat selects hiding places in rock shelters, caves, or heaps of fallen trees, visiting such places from time to time. Occasionally the shelter is shared with other individuals (Yudin and Yudina 2009).

Geographical Society Cave perhaps served as a shelter for tigers in the Late Pleistocene. After a successful hunt, a tiger carries its prey to neighboring thickets and lies down nearby in order to protect it from scavengers (crow, bear, fox) (Matiushkin 1974). In the Late Pleistocene, tigers could have hunted

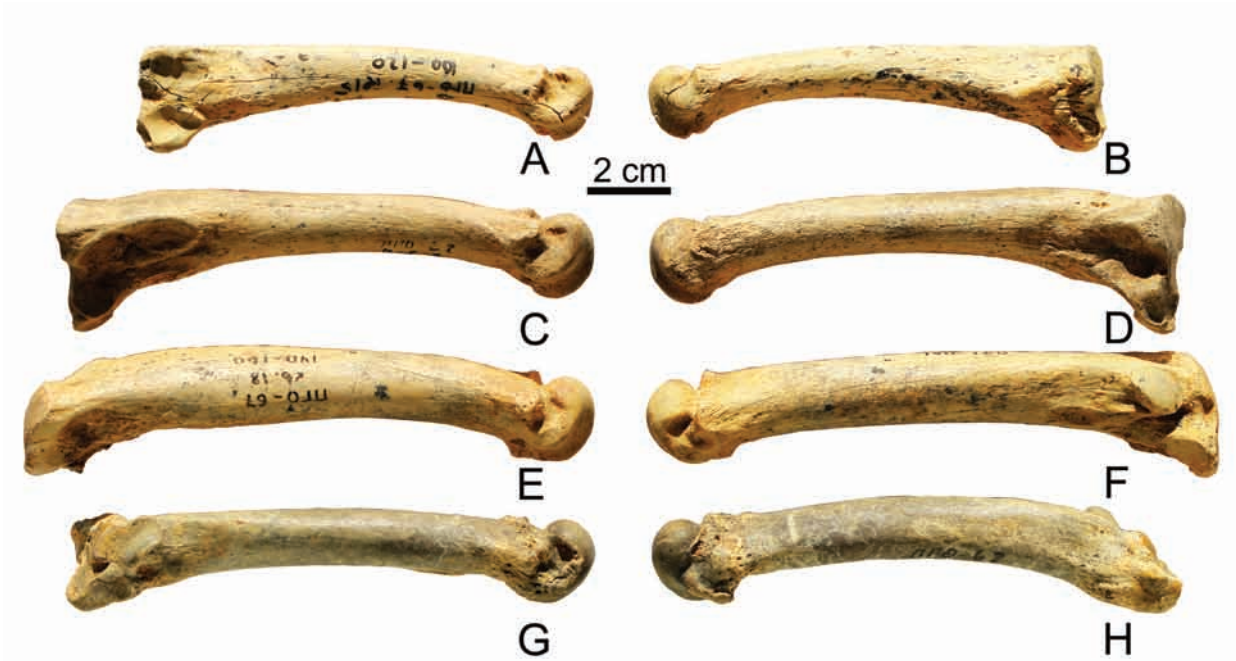

Fig. 12. *Panthera tigris* (A–D) and *P. spelaea* (E–H), Geographical Society Cave, tarsals (lateral (B, D, F, H) and medial (A, C, E, G) views; A, B – mt2 (ZIN 37288-52), right; C, D – mt3 (ZIN 37288-54), right; E, F – mt4 (ZIN 37933-1), right; G, H – mt5 (ZIN 37933-2), left.

near Geographical Society Cave and carried their prey into the cave. Judging from the milk teeth found there, this cave also served as a den for rearing young or as a place for hiding cubs. Females often hunt for smaller carnivores (badger, raccoon dog, and otter) on which to feed their young; bones of these animals have been recovered in Geographical Society Cave (Baryshnikov 2015).

The history of *P. tigris* is poorly known, being documented by a small number of fossil remains, which are, as a rule, fragmented. Genetic analysis demonstrates the genera *Panthera* and *Neofelis* to be sister taxa, having diverged approximately 6 Ma BP (million years ago) (Buckley-Beason et al. 2006; Johnson et al. 2006). Molecular cladograms for *Panthera* show *P. tigris* as a basal taxon separated from the lineage leading to *P. onca* (L., 1758), *P. leo*, and *P. pardus* (L., 1758) (Pecon-Slattery et al. 2004, Yu and Zhang 2005, Davis et al. 2010). The phylogenetic position of *P. uncia* (Schreber, 1775) remains insufficiently elucidated; whether it is affiliated with *P. leo* (Wei et al. 2009) or with *P. pardus* (Yu and Zhang 2005), or with *P. tigris* (Davis et al. 2010). The phylogenetic closeness of *P. tigris* and *P. uncia* suggests the early divergence of *Panthera* into two lineages. The development of one lineage (*P. onca*, *P. leo*, and *P. pardus*) is associated with Africa, where ancestors of recent species are recorded in the Late Pliocene (Laetoli), nearly 3.5 Ma BP (Werdelin and Levis 2005). Subsequently the representatives of this lineage had radiated over the Holarctic and later they reached the Neotropics. The second lineage (*P. tigris*, *P. uncia*) might have originated and developed in Asia, where the earliest remains of panther-like felids have been found in the Late Pliocene deposits of China (Yushe Basin) dated to 3.6–2.6 Ma (Qiu 2006). This dating coincides with the time of divergence of *P. uncia* and *P. tigris* hypothesized by molecular clock (Johnson et al. 2006, Davis et al. 2010). Representatives of the Asian lineage are not known beyond the bounds of Asia. The distinctiveness of this lineage is supported by the recent description of the fossil pantherin *P. blytheae* Tseng, Wang et al., 2013 from the Late Miocene–Early Pliocene of the Tibetan Himalaya which displays morphological similarity with *P. uncia* (Tseng et al. 2013). If this taxon definitely belongs to the genus *Panthera*, it may be hypothesized that the splitting of the African-Holarctic and Asian lineages occured in the Early Pliocene.

The morphological characters are also variously combined in recent and fossil pantherin species. For example, the cranial and cranial-dental features indi-

Table 12. Measurements (mm) of metatarsal bones in *Panthera*.

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd
	Mt 2						
	P. tigris						
Geographical Society Cave, Russia	ZIN 37288-52	108.7	19.2	24.9	13.2	19.9	17.7
	ZIN 37288-106	–	21.9	30.2	–	–	–
P. t. virgata, Turkestan, recent	ZIN 14997	116.2	21.6	27.2	14.0	21.0	21.1
P. t. sumatrana, zoo, recent, ♂	ZIN 30964	108.4	19.9	25.7	14.0	21.8	20.7
Zoo, recent	ZIN 1893	113.4	19.9	28.4	14.0	21.5	20.3
	P. spelaea						
Pobeda Cave, Ural, Russia	IEPA 467-n/n	130.4	26.3	30.2	16.1	–	–
	IEPA 467-n/n	129.1	28.6	–	16.5	24.8	–
	IEPA 467-3790	129.2	27.0	33.8	17.6	25.4	22.1
Secrets Cave, Ural, Russia	IEPA 810-n/n	131.7	25.9	34.2	16.9	25.4	22.9
	IEPA 810-n/n	131.8	25.0	–	16.1	22.8	–
Zapovednaya Cave, Ural, Russia	IEPA 639-15284	124.1	26.1	33.7	17.2	24.7	22.9
Zoolithen, Germany	NKHUB 30128	126.4	25.7	31.1	17.4	26.3	22.6
Dechenhöhle, Germany	NKHUB 30147	125.0	25.2	34.5	16.7	22.3	22.8
Hermannshöhle, Germany	NKHUB 14313	134.1	25.5	33.9	16.1	24.8	23.4
Groβwaplitz, Poland	NKHUB 9442	129.7	24.7	29.5	16.0	24.2	23.2
Srbsko Chlum Komin Cave, Czech Republic	NHMP R4537	113.5	23.1	28.9	15.0	22.1	20.1
	NHMP R4540	114.6	24.0	28.0	14.8	21.9	20.1
Malta, Angara River, Russia	ZIN 21846	118.4	22.8	28.8	16.0	22.6	21.5
Bolshoi Liakhovsky Island, Russia	ZIN 4224	117.5	21.8	30.3	15.7	23.1	21.7
	P. leo						
Zoo, recent, ♂	ZIN 30373	126.5	23.2	29.6	14.2	22.9	20.6
Zoo, recent	ZIN 4047						
	Mt 3						
	P. tigris						
Geographical Society Cave, Russia	ZIN 37288-54	127.8	24.7	34.1	18.7	24.1	20.7
	ZIN 37288-103	120.2	23.4	31.7	16.6	22.3	19.3
	ZIN 37288-104	124.0	23.6	31.0	15.5	22.6	19.2
	ZIN 37288-105	–	23.2	30.4	17.4	–	–
P. t. virgata, Turkestan, recent	ZIN 14997	129.7	25.6	33.2	17.1	24.7	20.3
P. t. sumatrana, zoo, recent, ♂	ZIN 30964	123.9	24.1	34.3	16.3	23.7	21.4
Zoo, recent	ZIN 1893	127.5	25.8	35.2	16.0	23.6	21.2
	P. spelaea						
Irtysh River, Western Siberia, Russia	IEPA 915-1469	146.6	30.4	41.6	24.0	28.5	25.8
	IEPA 915-2750	128.7	25.8	35.8	18.3	22.7	20.3
Pobeda Cave, Ural, Russia	IEPA 467-3789	126.2	26.2	–	17.9	–	–
	IEPA 467-5655	148.3	31.3	42.0	20.7	27.6	–

Table 12. *Continued*.

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd
	IEPA 467-3149	129.1	27.6	–	19.6	24.4	21.8
Freyburg, Germany	NKHUB 30136	137.2	29.5	39.9	19.8	27.0	–
Hermannshöhle, Germany	NKHUB 14312	141.8	28.8	39.8	19.6	26.7	24.0
	NKHUB 14315	137.4	28.8	37.8	20.5	26.5	25.1
Srbsko Chlum Komin Cave, Czech Republic	NHMP R4541	128.0	27.3	35.0	18.3	23.3	21.7
Malta, Angara River, Russia	ZIN 21846	118.4	22.8	28.8	16.0	22.6	21.5
Bolshoi Liakhovsky Island, Russia	ZIN 4224	117.5	21.8	30.3	15.7	23.1	21.7
	P. leo						
Zoo, recent, ♂	ZIN 30373	137.0	26.3	36.8	16.8	24.1	21.6
Zoo, recent	ZIN 4047	135.6	29.4	40.1	17.4	24.8	23.5
	Mt4						
Geographical Society Cave, Russia	ZIN 37288-93	–	22.0	29.2	–	–	–
	ZIN 37288-94	–	20.9	27.2	–	–	–
	ZIN 37288-95	119.5	20.5	24.1	14.1	20.2	19.1
	ZIN 37288-96	120.0	20.0	24.8	14.2	19.0	18.9
	ZIN 37288-98	–	21.4	24.3	15.9	–	–
	ZIN 37288-100	–	21.5	25.9	–	–	–
P. t. virgata, Turkestan, recent	ZIN 14997	127.5	22.7	23.3	13.9	20.8	19.6
P. t. sumatrana, zoo, recent, ♂	ZIN 30964	121.5	23.7	29.7	15.1	21.1	20.6
Zoo, recent	ZIN 1893	125.1	22.1	30.0	13.7	20.3	19.5
	P. spelaea						
Geographical Society Cave, Russia	ZIN 37933-1	135.2	23.8	30.2	17.7	23.1	21.4
Pobeda Cave, Ural, Russia	IEPA 467-n/n	143.1	28.2	35.3	18.3	24.9	23.4
Zapovednaya Cave, Ural, Russia	IEPA 639-9174	149.0	26.7	34.6	19.2	24.6	23.4
Verhnegubakhinski Grotto, Ural, Russia	IEPA 1069-655	137.5	30.6	34.4	17.7	23.9	23.7
Tiede, Gipsspalte, Germany	NKHUB 30140	130.7	27.8	30.1	16.8	22.7	22.0
Hermannshöhle, Germany	NKHUB 14316	142.4	26.9	36.9	17.4	24.6	23.9
Srbsko Chlum Komin Cave, Czech Republic	NHMP R4538	131.3	28.5	31.7	16.7	21.6	20.9
	NHMP R4642	131.9	26.4	31.3	17.3	22.0	21.0
Rebrov River, Dm. Laptev Strait, Russia	ZIN 35047	141.6	27.5	33.6	17.4	23.3	21.5
Duvanny Yar, Kolyma River, Russia	MMY 270	131.0	25.0	29.5	15.5	21.3	21.6
	P. leo						
Zoo, recent, ♂	ZIN 30373	139.5	26.2	31.9	15.1	21.9	20.9
Zoo, recent	ZIN 4047	137.4	27.5	33.6	15.6	21.9	23.0
	Mt 5						
	P. tigris						
P. t. virgata, Turkestan, recent	ZIN 14997	110.8	19.8	15.5	11.3	18.4	19.3
P. t. sumatrana, zoo, recent, ♂	ZIN 30964	108.5	21.2	17.3	12.2	18.6	19.5

Table 12. *Continued*.

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd
Zoo, recent	ZIN 1893	110.6	19.5	16.9	11.3	18.7	19.2
	P. spelaea						
Geographical Society Cave, Russia	ZIN 37933-2	124.7	23.9	20.0	14.2	21.2	21.4
Dechenhöhle, Germany	NKHUB 30148	131.4	24.5	16.9	13.3	20.1	–
	NKHUB 30141	138.6	28.9	17.8	14.4	22.7	21.2
	NKHUB 30142	142.9	31.9	21.1	15.8	24.8	23.1
Balve, Germany	NKHUB 30143	136.1	29.8	19.1	14.9	22.6	22.8
Hermannshöhle, Germany	NKHUB 14314	137.2	29.2	24.9	13.5	22.3	21.9
Srbsko Chlum Komin Cave, Czech Republic	NHMP R4539	120.7	20.5	25.9	13.9	20.7	18.9
	NHMP R4543	120.6	21.1	25.5	13.9	20.0	18.7
	P. leo						
Zoo, recent, ♂	ZIN 30373	125.4	27.4	18.7	12.2	20.5	19.2
Zoo, recent	ZIN 4047	124.2	26.6	21.0	12.9	20.9	21.6

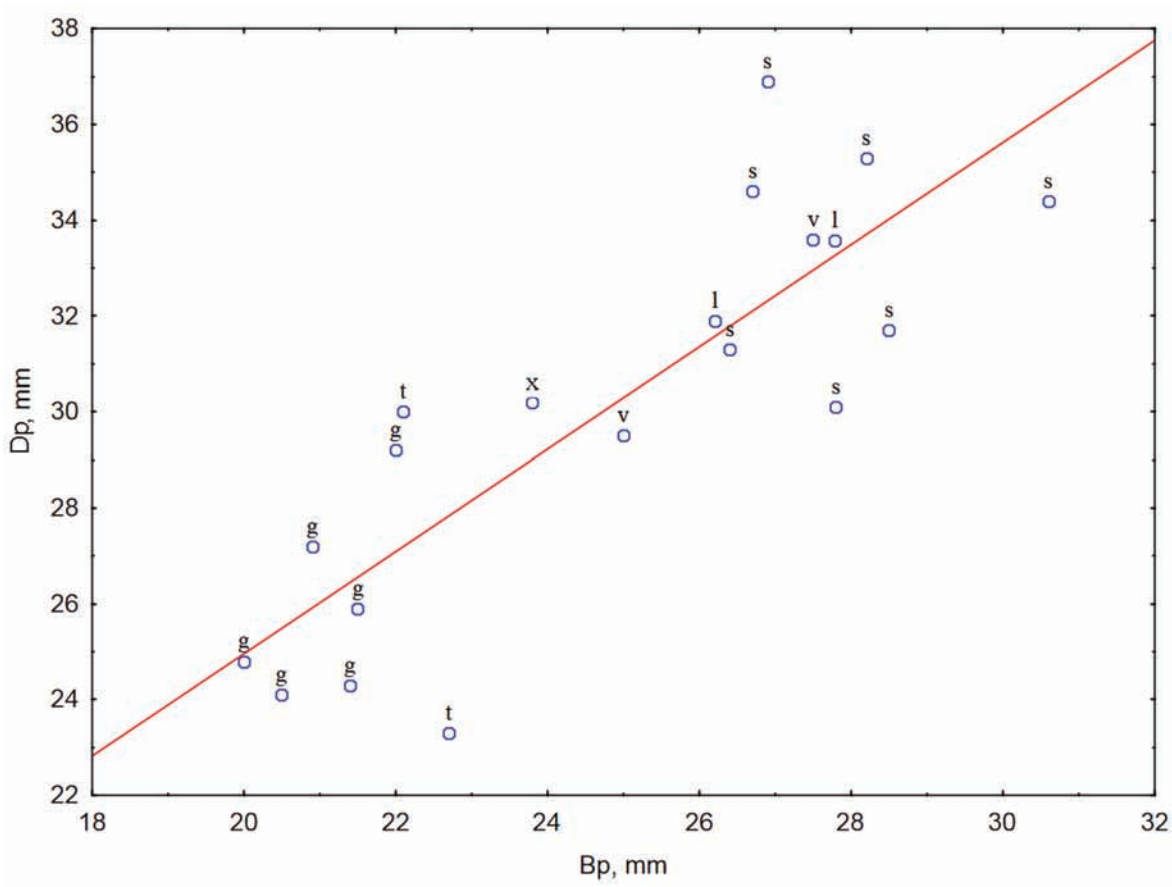

Fig. 13. Graphic relative to the relation between the breadth of the proximal end (Bp) and depth of the proximal end (Dp) in *Panthera* metatarsus 4 (mt4); g – fossil *Panthera tigris*, Geographical Society Cave, l – *P. leo*, s – *P. spelaea*, t – recent *P. tigris*, v – *P. spelaea veresh-chagini*, x – *P. spelaea*, Geographical Society Cave.

cate affiliation of *P. tigris* with *P. leo* and with the fossil American lion *P. atrox* Leidy, 1853, distinguishing these species from *P. uncia* (King and Wallace 2014), or separating the clade *P. tigris* + *P. uncia* from other representatives of the genus (Sakamoto and Ruta 2012). The cladogram based on the osteological, soft-part, and ethological characters divides *P. tigris* from the group of *P. onca* (L., 1758) + (*P. leo* + *P. pardus*) (Christiansen 2008). The basal position (with respect to them) is occupied by *P. uncia* and the fossil *P. palaeosinensis* (Zdansky, 1924).

The taxon *P. palaeosinensis* has been described on the basis of the skull with mandible from Henan (Locality 39) in China (Zdansky 1924). The lower carnassial tooth m1 has a metaconid shaped as a small cuspid. Later this species has been recorded in faunal assemblages from the Yangguo and Longdan localities in China, which are dated to 2.6–1.3 Ma (Qiu 2006). Various researchers regarded *P. palaeosinensis* as the ancestor of *P. tigris* (Hemmer 1967, 1968), considered this species as a primitive member of the lion or leopard clade of *P. leo* (Mazák 2010), or recognized the features of the Early–Middle Pleistocene jaguar-like felids in the mandible morphology (Sotnikova and Foronova 2014). Most probably, this taxon, which exhibits a combination of morphological characters of several recent species, belongs to an early radiation of the genus *Panthera* (Tseng et al. 2013). The holotype (MEU M3656) which I examined revealed the upper carnassial tooth P4 to be shorter (L=30.1 mm) and narrower (W=16.9 mm) than in Late Pleistocene *P. tigris*. No difference was detected in the length of the metastylar blade (37.9% of the greatest length). The preparastyle is pronounced (Fig. 5D).

The oldest representative of tiger-like panterins is thought to be *Panthera zdanskyi* regarded as a sister taxon of the recent tiger (Mazák et al. 2011). *P. zdanskyi* was described on the basis of the skull from the Longdan locality in Gansu province, North-Western China, whose age is evaluated as 2.55–2.16 MA. This jaguar-sized felid reveals the archaic tooth morphology: P4 has a distinctive ectoparastyle and a well-developed protocone, m1 shows a definite talonid, and the paraconid is large with respect to the protoconid (Mazák et al. 2011).

The earliest fossils of *Panthera tigris* from Asia are recorded in the Early Pleistocene of China (Yuanmou and Gongwangling) and Java Island (Trinil H.K. fauna). Tiger remains have been found in most Middle and Late Pleistocene sites of South-Eastern Asia, including Tam Hang, Punung, Niah Caves, Kecil, and Hang Hum (Hemmer 1971, Louys 2014). In the continental China, *P. tigris* is represented by bone remains from the Middle Pleistocene localities of Zhoukoudian (Locality 1) and Wanhsien, which were referred to *Felis acutidens* (Zdansky, 1928) (Zdansky 1928, Pei 1934, Hooijer 1947), as well as by remains from the Upper Pleistocene level of Zhoukoudian (Locality 3, Upper Cave) (Pei 1936, 1940). Their dental morphology and dental measurements show no difference from those of the fossil tiger in the examined material from Geographical Society Cave and Tigrovaya Cave; meanwhile, the samples from Wanhsien and Upper Cave are found to include also several larger specimens.

The mitochondrial analysis sorts out the recent populations of *Panthera tigris* into six clades (subspecies), one representing Amur tiger, *P. tigris altaica* (Luo et al. 2004). This analysis demonstrates a reduced genetic variability within the grouping of Amur tiger, which may be a result of the postglacial colonization of the region and the event of population bottleneck happened not earlier than 10,000 years ago (Luo et al. 2010). Presumably, one of the pathways of tiger migrations traversed through Central Asia, which is ascertained by a pronounced genetic similarity between Amur tiger and Caspian tiger, *P. tigris virgata* (Illiger, 1815) (Driscoll et al. 2009).

Another analysis embracing morphological, ecological, and molecular data revealed a great variation and marked overlapping of characters between the recent tiger populations as well as their low genetic diversity (Wilting et al. 2015). As a result of this analysis, it was proposed to accept only two subspecies: *P. tigris tigris* (L., 1858) in the continental part of Asia and *P. t. sondaica* (Temminck, 1844) in the islands of Sumatra, Java and Bali.

The lack of marked difference between the continental populations can be explained by the late migration of tiger to the northern regions of its distributional range. The Amur tiger appearance in Russian Far East could have occurred only in the Holocene, as shown by the above-mentioned morphological difference between *P. t. altaica* and the fossil tiger from Geographical Society Cave and others localities in the Primorskii Territory. Presumably, tiger traveled northwards on two occasions: firstly at a time of Late Pleistocene warming (MIS3) and secondly within the warm Holocene Interglacial. Tiger, most probably, did not occur in the region during

the cold climate conditions of the Last Glacial Maximum (approximately 18,000 years before present), which is in agreement with the reconstruction of the former distribution range of this species on the basis of palaeogeographic data (Kitchener and Dugmore 2000).

Therefore, the origin and evolution of the tiger is associated with Asia. The tiger has evolved as an inhabitant of dense forests and thickets. The tiger's unique bright coloration, reddish-rusty or yellow-rusty with transverse dark stripes, is adapted to the environment, with no analogues among other big cats. Notably, rock relief and dense, debris-strewn forest increase the chances of success when hunting (Matiushkin 1991).

The tooth morphology of the tiger and its ancestors is conservative in comparison with that of lions. *Panthera tigris*, *P. zdanskyi*, and *P. palaeosinensis* possess a P4 with a distinctive preparastyle whereas no preparastyle is seen in *P.* aff. *gombaszoegensis* from the Pliocene locality Laetoli in Tanzania (Barry 1987), or in *P. pardus* and *P. fossilis*. This feature is developed in *P. spelaea* and *P. leo* (Sotnikova and Nikolskiy 2006). *P. tigris* and *P. palaeosinensis* have a proportionally long metastylar blade on P4. In the lion-like lineage, *P. leo* and *P. pardus* have the metastylar blade slightly shorter than in *P. tigris*; the blade is still shorter in *P. spelaea*. Thus the tiger-like lines and lion-like lines reveal different trends in the transformation of their dentition. Lions show weakening of the trenchant function of carnassial teeth in comparison with tigers.

Teeth of fossil tiger from Geographical Society Cave are larger (especially m1) than these of the recent Far Eastern *P. tigris altaica*. The lower carnassial of the recent tiger seem to be more advanced that those of the Late Pleistocene tiger.

Therefore, the fragmentary osteological findings from the Late Pleistocene localities of the Russian Far East make it possible to define more precisely the history of the tiger at the north-eastern limit of its former distribution range. Tiger, apparently, did not spread far northwards, since genetic studies of numerous Late Pleistocene big-cat specimens from the permafrost of North-Eastern Asia and Alaska indicate that all specimens should be referred to *Panthera spelaea* (Ersmark et al 2015). Presumably, the restriction of tiger to forest regions as well as its individual hunting behavior prevented it from spreading onto the open landscapes of Northern Siberia and Beringia.

Panthera (*Panthera*) *spelaea* (Golfuss, 1810)

The cave lion is represented by a very small number of bone remains, which are described here for the first time. There are 6 specimens from at the least two individuals.

Description. The mandible ZIN 34930 (collector E. Leshok, 1972) is represented by the fragments of fused left and right dental bones (Fig. 14). The mandible which is of robust size (Table 1) can be ascribed to an adult male.

The symphysis is very long; with a total length of 76.6 mm, which exceeds the length of the symphysis in *Felis youngi* from Zhoukoudian 1 in China, although other dimensions of *F. youngi* are larger (Pei 1934). The specimen ZIN 34930 has two canines, two premolar rows p3–p4, and the broken fragment of right the m1. The mandible lower margin and coronoid process are partly damaged: the mandible was gnawed by a large carnivore, most probably by hyena. The same damage is seen on the mandible of *F. youngi* (Pei 1934: pl. XXXIII, *1c*).

ZIN 34930 displays two mental foramina situated below the postcanine diastema (the anterior) and below p3 (the posterior). A small "chin" is distinguishable, which is known to occur in *P. tigris* and *P. spelaea*. The posterior margins of both canines show wear facets. The canine apices and the main cusp of p4 are also markedly worn.

The examined material also includes the small left mandible fragment (ZIN 37931, recovered from layer 2), which displays the complete row of cheek teeth p3–m1 (p4 is partly broken). The mandible lower margin was bitten off by a large carnivore (Fig. 15).

The tooth morphology of both specimens is characteristic of *P. spelaea*. The lower premolar p3 does not differ from premolars of *P. tigris* in the length, being, although significantly wider (Table 8). The ratio between the width and length of the p3 tooth crown is 53.3% and 56.5%, which conforms more closely to *P. spelaea*, than to *P. tigris*. The anterior cusp of p4 is slightly turned in ZIN 34930 (Fig. 7C) or its anterior ridge nearly coincides with the tooth long axis, as in *P. spelaea* (ZIN 37931).

The isolated tooth m1 (ZIN 37932, recovered from a depth of 30 cm) has a slightly convex lingual wall (Fig. 15), which is regarded as a distinctive feature of *P. spelaea* and P. *leo* (Vereshchagin 1971). Although this character may be expressed in varying degrees in *P. spelaea*, it is absent in *P. tigris*. The tooth

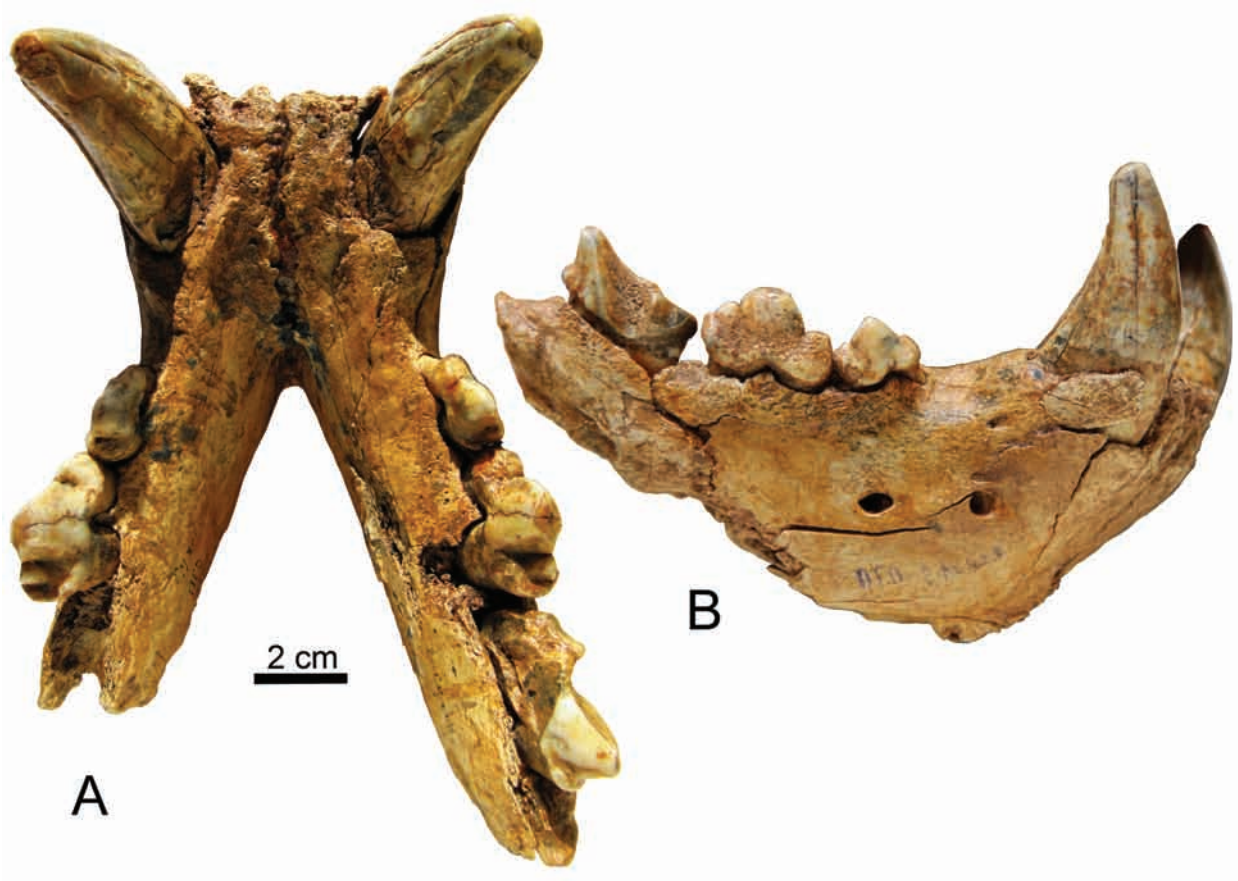

Fig. 14. *Panthera spelaea*, Geographical Society Cave, mandible (ZIN 37930); occlusal (A) and buccal (B) views.

crown ZIN 37932 is wide (Table 8); the ratio between its width and length is 54.5%, as in *P. spelaea*.

The lower canine (ZIN 37933-4, recovered from a depth 170–200 cm) and postcranial bones: os patella (ZIN 37933-3, layer 5), mt4 (ZIN 37933-1, depth 140–160 cm), and mt5 (ZIN 37933-1, layer 5) are provisionally referred to *P. spelaea* as their large dimensions exceed those of males in recent *P. tigris* (Tables 11, 12).

The forth metatarsal (ZIN 37933-1; Fig. 12E, F) has the articular facet which attaches to the os cuboideum, which resembles that of *P. tigris*. However, the same articular facet shape was observed in the specimen of *P. spelaea vereshchagini* found on the Arctic coast of Siberia (Rebrov River, ZIN 35047).

The fifth metatarsal bone (ZIN 37933-2; Fig. 12G, H) corresponds in size to the smallest specimens of *P. spelaea* (Table 12). The proximal end exhibits two lobes divided by an incision; the medial lobe is somewhat widened, as in *P. tigris* (this incision is incon-

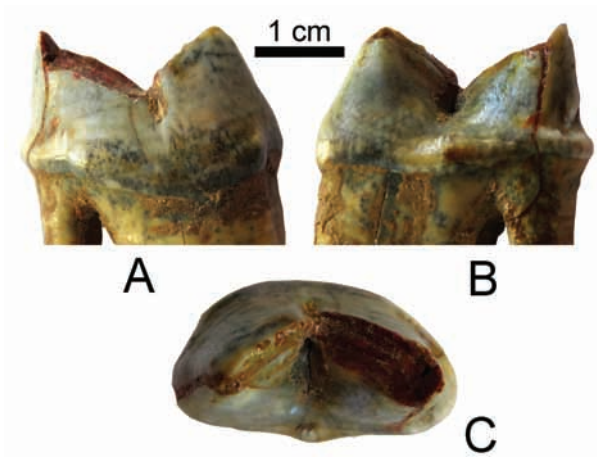

Fig. 15. *Panthera spelaea*, Geographical Society Cave, right m1 (ZIN 37932); buccal (A), lingual (B) and occlusal (C) views.

Fig. 16. *Panthera tigris*, Geographical Society Cave, left ulna (ZIN 37288-49) with tooth-marks of large carnivore (possible, wolf); medial view.

spicuous in *P. leo* and the medial lobe of the proximal end is more strongly flattened and widened).

Conclusions. In the Late Pleistocene, the cave lion (*Panthera spelaea*) was widespread in Northern Eurasia from the Atlantic to the Pacific seacoast, reaching across the Beringian land bridge. The southern limit of its distribution range runs from the Mediterranean to Kazakhstan, and Southern Siberia (Altai, Transbaikalia) (Vereshchagin 1971). The southern part of Russian Far East seems to be the southeastern extremity of the vast distribution range species. Cave lion has been also recorded in North-Eastern China (Manchuria) and in Northern Korea (Park 1988, Kahlke 1994).

Unfortunately, the absence of reliable stratigraphic information on the fossil remains means that we cannot say whether the cave lion (inhabitant of open landscapes) and the tiger (forest dweller) co-existed in the vicinity of Geographical Society Cave or if these two species were separated in time. In any case the scarcity of lion fossils indicates its rarity in the southern parts of the Russian Far East. Remarkably, the lion mandibles from Geographical Society Cave have been gnawed by a large carnivore. The tooth marks resemble those on the hyena mandibles found in this cave (Baryshnikov 2014); presumably, marks might have been made in both cases by the fossil hyena *Crocuta ultima* (Matsumoto, 1915). In contrast the tiger remains reveal no traces of hyena tooth marks. Hyena tooth marks were also not found on the tiger bones from Tigrovaya Cave. The ulna fragment of the fossil tiger from Geographical Society Cave (Fig. 16) probably has been gnawed by wolf (*Canis lupus* L., 1758).

Molecular genetic analysis has revealed two lion clades: 1) extinct *P. spelaea* and *P. atrox*, and 2) extant *P. leo* (Burger et al. 2004; Barnett et al. 2009). The date of the divergence between the lineages of extinct and extant lions is estimated at nearly 600,000 years ago (Burger et al. 2004), whereas *P. atrox* was found to have diverged from cave lions about 340,000 years ago (Barnett et al. 2009).

The earliest lion-like large felids are known from Africa not before 1.7 Ma (Hemmer 2011). The ancestor of cave lion is thought to have been the very large species *Panthera fossilis* von Reichenau, 1906 which migrated from Africa to Eurasia in the early Middle Pleistocene; this species is regarded also as the ancestor of *P. atrox* (Sotnikova and Nikolskiy 2006, Sabol 2011). Asiatic finds of *P. fossilis* are scant. Sotnikova and Foronova (2014) the left mandible fragment from Bachatsk Quarry in Western Siberia and mandible from Zhoukoudian (Locality 1) in China referred to this species. The latter mandible was originally described as *Felis youngi* (Pei 1934). The tooth dimensions of *Felis youngi* correspond with those of female *P. fossilis* from European localities (Sabol 2014). However, the European finds of *Panthera spelaea* from earlier in the Pleistocene are also characterized by large size; in a course of evolution of this species in the Middle and Late Pleistocene a decrease in size process is observed (Argant et al. 2007, Baryca 2008, Marciszak et al. 2013).

The time of appearance of *P. spelaea* in Asia is not yet clear. Most probably, was in the Middle Pleistocene; as was determined for the remains of a big cat from Yakutia (Mamontovaya Gora), which is morphologically similar to *P. spelaea* (Boeskorov and Baryshnikov 2013).

Panthera (*Panthera*) *pardus* (Linnaeus, 1758)

Ovodov (1977) assigned 31 fossil remains from Geographical Society Cave to leopard, representing at least two individuals. I found that most of them belong to lynx (*Lynx lynx*), which is known to attain a large size in the Late Pleistocene. I conditionally refer 10 fossil bones to leopard. These comprise phalanges and small fragments of postcranial bones resembling in size those of *Panthera pardus*. However, there is no certainly that this species is present in the faunal assemblage of Geographical Society Cave.

Description and comparison. The fossil remains, which reliably belong to *Panthera pardus*, have been recovered from Letuchaya Mysh Cave. Ovodov (1977) dates this locality to the Late Pleistocene; meanwhile, the absence of the remains of hyena, mammoth, horse, rhino, and bison provides grounds to refer the formation of cave deposits to the final part of Pleistocene.

The right mandible fragment with p3–m1 and with the canine alveolus (ZIN 37296, Fig. 17) exceeds in size this bone in males of recent leopard occurring in the southern part of the Russian Far East and in China (Table 13). The length of the tooth row p3–m1 of the fossil leopard measures 54.7 mm; whereas the tooth row in males of the subspecies *P. pardus orientalis* (Schlegel, 1857) from the Primorskii Territory of Russia varies from 46.9 mm to 51.1 mm (mean 48.7 mm, n=9). ZIN 37296 is more robust than the fossil leopard mandible from the Caucasus (Kudaro 3 Cave) (Baryshnikov 2011); however, the specimen is markedly smaller in comparison with the mandible of *Felis* cf. *pardus* from the Middle Pleistocene locality of Zhoukoudian 1 in China (Pei 1934). The leopard from the Late Pleistocene Upper Cave locality in Northern China (Pei 1940) has similar tooth dimensions to those of ZIN 37296.

The lower carnassial tooth m1 ZIN 37296 has no metaconid and its talonid is not developed. The tooth is somewhat larger (with respect to p4) than that of *Panthera* cf. *pardus* from Zhoukoudian 1 and recent *P. pardus orientalis*.

Discussion. At the present time, leopard has a widespread distribution in Africa, Southern and South-Eastern Asia, extending northwards to the Caucasus, Tajikistan, and the southern part of the Russian Far East. In the Late Pleistocene of Europe, leopard occurred as far as Berlin (Diedrich 2013).

The earliest records of *P. pardus* are known from Africa, dated to approximately 2.0 Ma (Werdelin and Levis 2005). Molecular phylogenetic analysis suggests that the modern *P. pardus* lineage in Africa probably originated 470,000–825,000 years ago and

Table 13. Measurements (mm) of mandibles of *Panthera pardus*.

Measurements	*P. pardus*			*P.* cf. *pardus*	
	Late Pleistocene	Recent		Middle Pleistocene	
	Russian Far East	*P. p. orientalis*	*P. p. delacouri*	China	
	Letuchaya Mysh	Primorskii Territory	Kham, Tibet, China	Zhoukoudian 1	
	ZIN 37296	ZIN 18369, ♂	ZIN 18394, ♂	(Pei 1934)	
Lc1-m1	101.6	74.3	80.1		
Lp3-m1	54.7	46.9	50.3	62.0	
Height behind m1		28.7	32.2	39.8	36.0
Height before p3	33.8	25.7	28.1	41.5	35.5
Teeth					
Lp3	14.9	11.5	12.7	16.3	
Wp3	8.1	6.7	6.3	9.0	
Lp4	20.8	17.9	19.3	23.2	21.5
Wp4	9.9	9.4	9.7	12.0	11.1
Lm1	22.4	18.9	20.3	24.0	22.0
Wm1	10.9	8.9	8.6	12.2	10.7

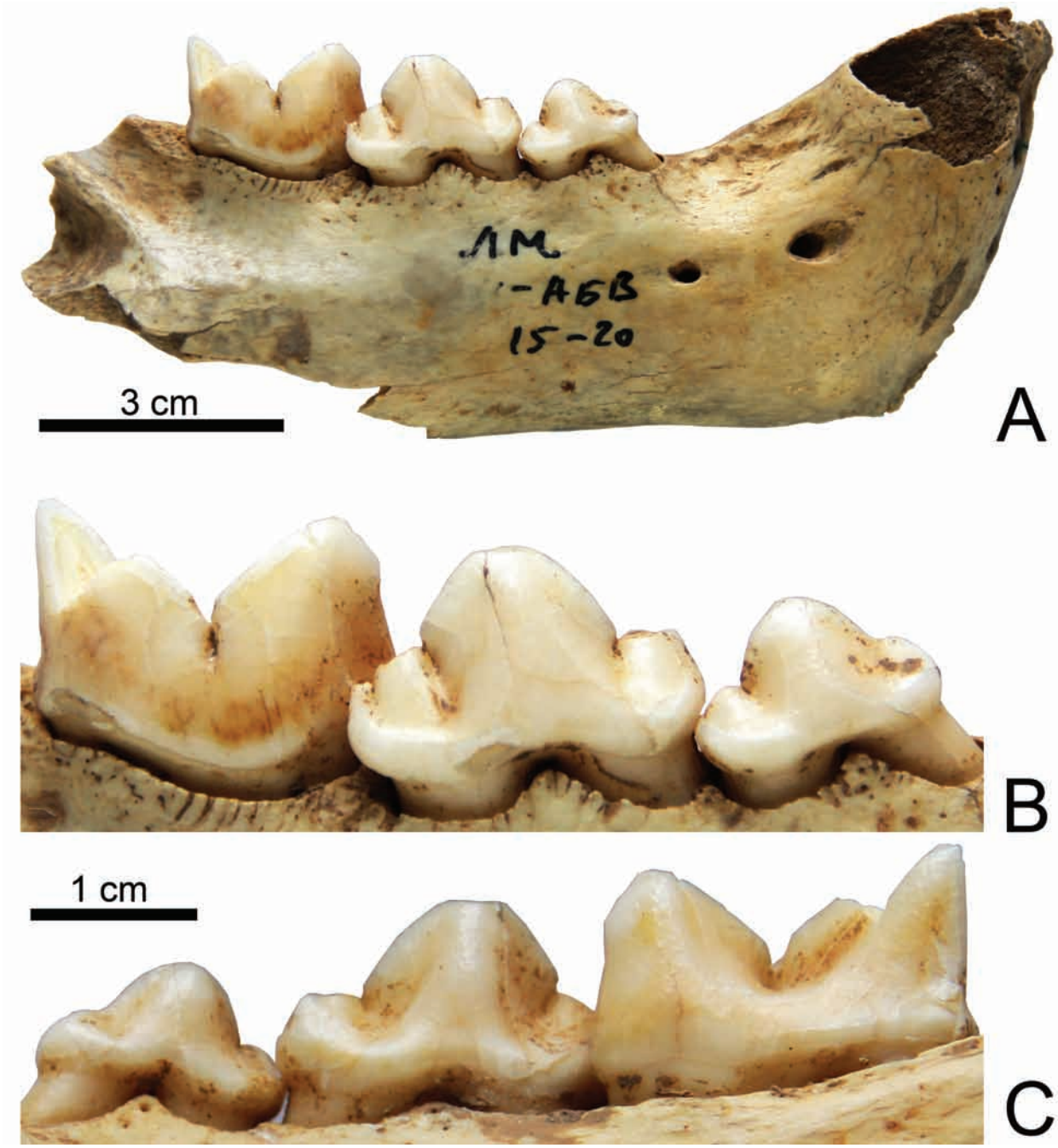

Fig. 17. *Panthera pardus*, Letuchaya Mysh Cave, left mandible (ZIN 27296) (A) and lower teeth p3–m1 (B, C); buccal (A, B) and lingual (C) views.

the subsequent leopard migration onto and across Asia occurred roughly 170,000–300,000 years ago (Uphyrkina et al. 2001). This conforms with the presence of leopard in the Middle Pleistocene localities of Europe (Mauer), Caucasus (Kudaro 1 Cave), China (Zhoukoudian 1), and Java (Ngandong) (Pei 1934, Kurtén 1968, Hertler and Volmer 2008, Baryshnikov 2011). In Eastern Asia, leopard fossils become widespread in Late Pleistocene localities (Louys 2014), as far north as Letuchaya Mysh Cave.

Genus *Lynx* Kerr, 1792

***Lynx lynx* (Linnaeus, 1758)**

Ovodov (1977) recorded 31 lynx bones belonging to two individuals from Geographical Society Cave. I referred 51 bone remains to lynx. Such an abundance of the lynx remains is unusual for Late Pleistocene localities in Russia.

Description. There material includes a lower canine and several short limb bones, including phalanges (Fig. 18). The lower canine (ZIN 37278-5, depth 180–190 cm) is typical in size for *Lynx lynx* (length 10.2 mm, width 7.5 mm). Bones of the limb distal parts (metacarpals, talus, metatarsals) are similar in their maximum length to those of males of the recent lynx, being, although more massive (Table 14).

Many of the lynx remains were recovered from the lower part of the cave deposits, at a depth of 190–210 cm and 250–300 cm. One phalanx displays signs of acidic corrosion, having probably passed through the gut of a hyena or tiger; however, other bones have no traces of similar damage by large carnivores. The lynx might be occasional prey of tiger, as was observed for lynx in the Primorskii Territory (Kaplanov 1948).

Discussion. Lynx (*Lynx lynx*) inhabits the forest zones and mountain areas of Northern Eurasia as far south as the Himalayas. In Siberia, its fossil finds are confined to the southern regions, where lynx fossils are recorded from the Late Pleistocene localities of Altai (Denisova Cave) and the Sayan Mountains (Nizhneudinskaya Cave). The only northern is from the Kolyma Lowland (Bolshaya Kuropatochiya River, 70–71°N), Yakutia. This presumably results from a northern migration of lynx in a warm Interstadial, when the forest zone shifted northwards (Boeskorov and Baryshnikov 2013). The absence of forest and shrubbs on the Beringian land bridge explains why *L. lynx* did not disperse to Alaska.

The ancestor of recent lynx is considered to be *Lynx issiodorensis* (Croizet et Jobert, 1828) from the Late Pliocene and Early Pleistocene of Eurasia and North America (Werdelin 1981). In Western Europe, this species is regarded as ancestral to *L. pardina* (Temminck, 1827), which is represented in the Late Pleistocene by the subspecies *L. pardina spelaea* (Boule, 1910). There is also the Asian taxon *L. shansius* (Teilhard et Leroy, 1945), which is quite often treated as the subspecies *L. issiodorensis shansius* (Werdelin 1981). The descendant of the latter which appears to be *L. lynx*, dispersed to Europe in the Last

Fig. 18. *Lynx lynx*, Geographical Society Cave; lateral (A, B), medial (C) and dorsal (D) views. A – metatarsal 2 (mt2), left (ZIN 37278-25); B – metacarpal 2 (mc2), left (ZIN 37278-3); C – metacarpal 5 (mc5), left (ZIN 37278-1); D – talus, right (ZIN 37278-24).

Table 14. Measurements (mm) of limb bones in *Lynx lynx*.

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd	GB
		Mc2						
Geographical Society Cave, Russia	ZIN 37278-1	68.1	11.6	14.4	7.9	13.1	11.1	
L. l. lynx, Leningrad Province, ♂, recent	ZIN 34307	67.4	10.5	13.6	6.5	11.9	10.6	
		Mc5						
Geographical Society Cave, Russia	ZIN 37278-2	–	10.0	14.0	6.6	–	–	
	ZIN 37278-3	60.5	11.3	11.4	7.5	11.5	10.3	
L. l. lynx, Leningrad Province, ♂, recent	ZIN 34307	59.3	9.8	10.9	6.5	10.8	10.2	
		Talus						
Geographical Society Cave, Russia	ZIN 37278-24	31.2						21.9
L. l. lynx, Leningrad Province, ♂, recent	ZIN 34307	28.4						25.6
		Mt2						
Geographical Society Cave, Russia	ZIN 37278-25	95.8	12.2	15.2	8.9	15.0	12.6	
	ZIN 37278-4	–	–	–	7.2	12.8	10.5	
	ZIN 37278-27	–	11.6	14.8	9.0	–	–	
L. l. lynx, Leningrad Province, ♂, recent	ZIN 34307	94.3	10.9	13.5	7.0	13.3	11.9	
		Mt3						
Geographical Society Cave, Russia	ZIN 37278-26	–	15.3	18.6	11.0	–	–	
L. l. lynx, Leningrad Province, ♂, recent	ZIN 34307	103.7	14.6	18.1	9.5	13.2	12.8	

Interglacial (Eem) (Baryca 2008). The Zhoukoudian 1 locality in China is the type locality of the lynx-like taxon *Felis teilhardi* (Pei, 1934); its limb bones were slightly smaller than in recent *Lynx lynx* (Pei 1934).

The genetic molecular analysis revealed the presence of three haplogroups within the recent *L. lynx*, more ancient lynx lineages being found in Central Asia (Rueness et al. 2014). The animals from Russian Far East are referred to the same haplogroup as lynxes from eastern Siberia. The spread of lynx in the Postglacial arose from several refugia.

CONCLUSIONS

The examination of paleontological collection from Geographical Society Cave and several neighboring caves revealed the presence of four felid species in the Late Pleistocene of the southern part of the Russian Far East: *Panthera tigris*, *P. spelaea*, *P. pardus*, and *Lynx lynx*. All species, excepting *P. spelaea*, occur in the region now.

The absence of detailed stratigraphic correlation for the bone material precludes the possibility of demonstrating the coexistence of big cats: *Panthera tigris* and *P. spelaea*. In conditions of mosaic mountain landscape in the vicinity of the cave, the forest dwellers (*Panthera tigris, P. pardus, Lynx lynx*) could coexist with inhabitants of open vegetation (*Panthera spelaea* and the fossil hyena *Crocuta ultima* (Matsumoto, 1915)). However, it is not improbable that species with different ecological preferences were confined to different stratigraphical levels.

The remains of felids and other Carnivora have been found in Geographical Society Cave within sediments formed during a warm Interstadial within MIS 3. The remains of southern species (*Panthera tigris*, *Crocuta ultima*) are represented there by large bone accumulations, whereas the fossils of boreal species (*Panthera spelaea*, *Martes zibellina* (L., 1758), *Gulo gulo* (L., 1758)) are scant. Most probably, *Panthera tigris* and *P. pardus* lived in the southern parts of Russian Far East only in warm climatic conditions (Interstadial, Interglacial), when the region had been predominantly forested; presumably, these species were absent in the region in colder periods of glaciations.

The fossil material from Geographical Society Cave comprises 12 carnivore species and numerous

tooth-marks of large Carnivora are present. Undoubtedly, carnivores actively participated in the bone accumulation in the cave. The Geographical Society Cave could have served as a shelter for tiger, wolf, and hyena and was a maternity den for hyena and tiger (Baryshnikov 2014, 2015a, b). Brown bears (*Ursus arctos* L., 1758) also died in the cave during winter hibernation (Baryshnikov 2015b). Such taphonomic diversity suggests that Geographical Society Cave, in different times of its history (or in different seasons), was used by various carnivores for diverse purposes. From time to time it was visited by hominins; however, the intensive use of this karst cavity by carnivores indicates that visits of ancient people were only short-term.

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