

Notes on carnivore fossils from the Pliocene Udunga fauna, Transbaikial area, Russia

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Abstract

We provide notes of carnivore fossils from the middle Pliocene Udunga fauna, Transbaikial area, Russia. The fossil carnivore assemblage consists of more than 200 specimens including eleven genera. *Ursus*, *Parailurus*, *Parameles*, and *Ferinestris* are representative of the animals of thermophilic forest biotopes. On the other hand, *Chasmaporthetes* and *Pliocrocuta* are probably specialized in open environment. The prosperity both in forestal and semiarid carnivores indicate that the Udunga fauna is comprised of mosaic elements.

Introduction

The fauna dating back to the Pliocene in Udunga, Transbaikalia, Russia, comprises eleven species of mammals, such as rodents, lagomorphs, carnivores, perissodactyls, artiodactyls, and elephants (Kalmykov, 1989, 1992, 2003; Kalmykov and Maschenko, 1992, 1995; Vislobokova *et al.*, 1993, 1995; Erbajeva *et al.*, 2003). The Udunga site is located on the left bank of the Temnik River, the tributary of the Selenga River in the vicinity of Udunga village (Figure 1). This mammal fauna is discovered from the red clayey beds of the Upper Neogene Chikoi Formation (Kalmykov, 1989; Erbajeva *et al.*, 2003).

The fossil materials of the Pliocene Transbaikalian carnivores have been studied by many workers (e.g. Kalmykov, 1989, 1992, 2003; Sotnikova and Kalmykov, 1991; Vislobokova *et al.*, 2001; Sotnikova, 2006, 2008), and these series are their ongoing research. Their works show the rich diversity of carnivores in the Pliocene Transbaikalian area and the richness is particular feature of the Udunga fauna. In this study, we remark eleven genera of carnivores from the Udunga locality, which have been recognized from the materials stored in the Southern Scientific Center (SSC), Rostov-on-Don, Russia. The preliminary study of carnivorous mammals of Udunga fauna was reported by Sotnikova and Kalmykov (1991),

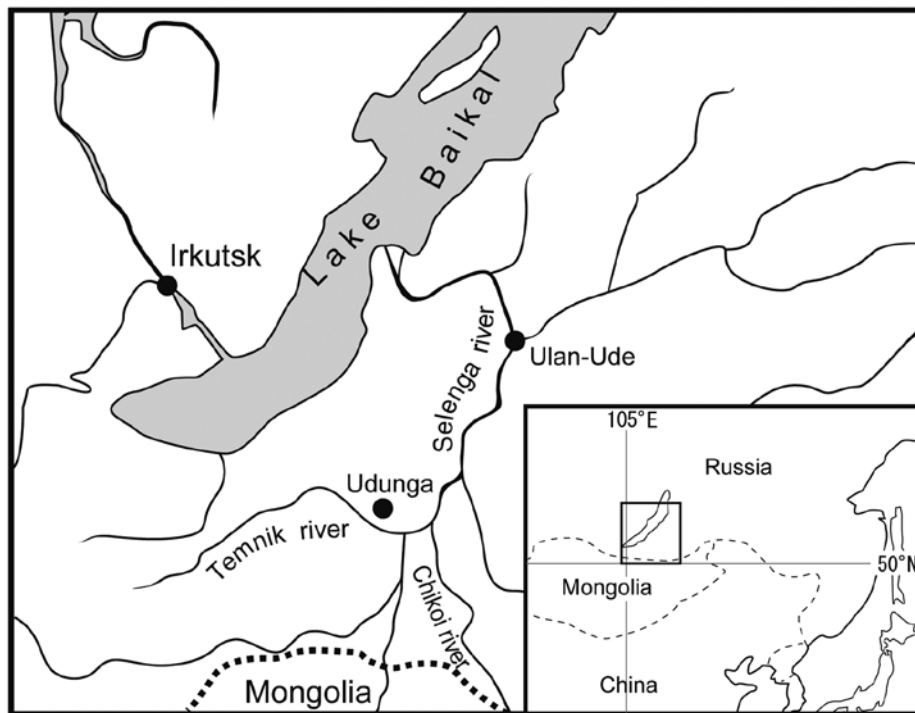


Figure 1. The location of the Transbaikal area. Modified from Kalmykov (2002).

but *Canis* sp., *Gulo minor* are not stored in SSC collection. The recognized species in this study are listed in Table 1.

Remarks

Order Carnivora Bowdich, 1821

Family Canidae Gray, 1821

Genus *Nyctereutes* Temmnick, 1838

***Nyctereutes* sp. indet.**

Sotnikova and Kalmykov (1991) reported the occurrence of *Nyctereutes* from the Udunga fauna. Three hemimaxillae, four hemimandibles, isolated M^2 , and three of isolated M_1 of *Nyctereutes* are distinguished from the SSC collection (Table 2). There are a few *Nyctereutes* materials known in the Udunga fauna, which is identified as *Nyctereutes* sp. (Sotnikova and Kalmykov, 1991; Kalmykov, 1992, 1999, 2003; Erbajeva *et al.*, 2003; Kalmykov, Maschenko, 2005, 2006; Kalmykov *et al.*, 2005; Maschenko *et al.*, 2007). The oldest representative of the genus *Nyctereutes* (*N. aff. donnezani*) is known from late Turolian Venta del Moro (Spain), so the origin is considered to appear in western part of Palaearctic region (Morales and, Aquirre, 1976). In Ruscinian, they were widespread in Europe (Alcalá and Montoya, 1989-1990; Tedford, 1995). Early representatives of *Nyctereutes* (*N. donnezani*) are known from La Gloria 4 (MN 14), La Calera (MN 15a), Layna (MN 15b),

Table 1. List of carnivore fossils of the Udunga fauna stored in SSC collection.

taxon	number of specimens	references
<i>Nyctereutes</i> sp. indet	11	Sotnikova and Kalmykov (1991)
<i>Canis</i> sp. indet.	2	Sotnikova and Kalmykov (1991)
<i>Ursus minimus</i>	8	Sotnikova and Kalmykov (1991)
<i>Pannonictis</i> sp. indet.	8	Vislobokova et al (2001)
<i>Parameles suillus</i>	5	Kalmykov (1989)
<i>Ferinestris</i> sp. indet.	107	Sotnikova (2006)
<i>Parailurus baikalicus</i>	3	Sotnikova (2008)
<i>Pliocrocota pyrenaica</i>	30	Kalmykov (1989)
<i>Chasmaporthetes lunensis</i>	4	Vislobokova et al (2001)
<i>Lynx shansius</i>	28	Kalmykov (1989)
<i>Homotherium</i> sp. indet.	2	Kalmykov (1989)

Table 2. Specimens of *Nyctereutes* sp. indet.

Udg-	side	Material
43	R	maxilla with M ¹
48	R	mandible with M ₁ -M ₃
49	L	mandible with P ₄ and M ₁
50	R	maxilla with P ⁴ -M ²
119	R	mandible with lower canine, P ₂ , P ₄
161	R	maxilla with P ₃ and P ₄
162	R	M ₁ (broken)
163	L	M ₁
190	L	M ²
##	R	mandible with M ₁
##	R	M ₁

Table 3. Specimens of *Canis* sp. indet.

Udg-	side	Material
176	L	mandible with M ₂
2471		upper and lower dentitions

Spain. Later form, *N. megamastoides* is from Villarroja (MN 16a), El Rincon (MN 16b), La Puebla del Valverde (MN 17a), Spain (Alcalá and Montoya, 1989-1990). *Nyctereutes* is also known from the western Transbaikalia area (Sotnikova and Kalmykov, 1991, Kalmykov, 1992) and China (Tedford, Qiu, 1991; Tong *et al.*, 1995; Li *et al.*, 2003) in Villafranchian. In Central to East Asia, *N. cf. sinensis* is known from western Transbaikalia (Beregovaya), and *N. megamastoides* is known from the northern Mongolia (Shamar) (Sotnikova, 1976). Tedford and Qui (1991) hypothesized that the early Pliocene Chinese and European *Nyctereutes* should be organized in the same taxon. *N. megamastoides* diverged from *N. donnezani* at the late Pliocene in Europe (Soria and Aguirre, 1976), which is morphologically comparable with *N. sinensis*. On the other hand, *N. tingi*, which is known from East Asia and suddenly occurred in the early Pliocene, is closely related to extant *N. sinensis* (Tedford and Qui, 1991). Thus, identification of *Nyctereutes* from the Udunga fauna would be important for understanding relationship between European and Asian taxon in Pliocene.

Genus *Canis* Linnaeus, 1758

Canis sp. indet.

Only two specimens of large canid are available in the SSC Udunga collection (Table 3). Left mandible with M₂ (Udg-0176) and isolated upper and lower dentitions (Udg-2471)

Table 4. Specimens of *Ursus* sp. indet.

Udg-	side	Material	Udg-	side	Material
16	R	lower canine	2001		upper canine
53	L	M ₂	2002	L	M ₁
54	R	M ₂	2003	R	M ₂
140	L	maxilla with P ⁴	2004	R	M ₃

Table 5. Specimens of *Pannonictis* sp. indet.

Udg-	side	Material
128	L	maxilla with P ⁴
129	R	maxilla with P ³ and P ⁴
144	R	P ⁴
145	R	M ¹
150	L	P ⁴
2400	R	upper canine
2410	L	upper canine
2400	L	lower canine

are obviously larger than *Nyctereutes*. These specimens are considered *Canis* but there are some small forms. *Canis* appeared in Eurasia in the middle Turolian (Mein, 1990), but their adaptive radiation occurred in Ruscinian (Vangengeim *et al.*, 1998). Its oldest representatives are known from Europe such as Los Mansuetos, Concud (*C. cipio*, MN 12), Perpingnan (*C. michauxi*, *C. adoxus*, MN 15), La Calera (*C. indeterminado*, MN 15a), Odessa catacombs (*C. petenyi*, MN 15), Villarroja (*C. indeterminado*, MN 16a), Kuruksai (*C. kuruksaensis*, *C. ex gr. lephagus*, MN 16b), Kvabebi (*Canis* sp., MN 16), Etouaires (*C. etruscus*, MN 16b) (Vekua, 1972; Vangengeim *et al.*, 1988; Alcalá and Montoya, 1989-1990; Mein, 1990). In China, *Canis* appeared in the late Ruscinian (Tedford, 1995; Tedford, Qiu, 1996).

Family Ursidae Fisher de Waldheim, 1817

Genus *Ursus* Linnaeus, 1758

Ursus minimus Devèze et Bouillet, 1827 (Stuart, 1982)

Sotnikova and Kalmykov (1991), Kalmykov (1992) reported *Ursus ex gr. ruscinensis-minimus* from the Udunga fauna. Seven isolated teeth including upper canine, lower canine, M₁, M₂, M₃, and a left maxilla with P⁴, are stored in the SSC Udunga collection (Table 4). *U. minimus* retains primitive morphological characteristics, which is closely related to the late Ruscinian or the earliest Villafranchian ursid forms (Sotnikova and Kalmykov, 1991; Kalmykov, 1992; Sotnikova, 2006). *U. minimus* Deveze et Debouillet (sin. *U. arvernensis* Croizet et Jobert) is known from three locality, such as Gaville (Val de'Arno, Italy), Puy de Dôme (France) and Layna (Spain) (Torres, 1988).

The identification of the Pliocene Russian ursid is disputed (Vekua, 1972; Sotnikova and Kalmykov, 1991; Kalmykov, 1992; Vislobokova *et al.*, 1993; and Sotnikova, 2006). In Europe *Ursus* is known from the late Ruscinian localities, such as Layna (*U. ruscinensis*), Odessa catacombs (*U. arvernensis*), Weze (*U. wenzensis*) (Kowalski, 1990; Mein, 1990; Perez, Soria, 1989-1990; Vangengeim *et al.*, 1998). In China *Ursus* sp. is known from Ertente (*Ursus* sp.). The stratigraphical range of genus *Ursus* is from the late Turolian to the present.

Family Mustelidae Fischer de Waldheim, 1817

Table 6. Specimens of *Parameles* sp. indet.

Udg-	side	Material
2	L	mandible with lower canine-M ₂
3	L	mandible with lower canine-M ₂
177	L	mandible with lower canine, P ₄ , M ₁
178	L	mandible with M ₁ and M ₂
2420		upper canine

Subfamily Galictinae Reig, 1957**Genus *Pannonictis* Kormos, 1931*****Pannonictis* sp. indet.**

Vislobokova *et al.* (2001) reported the occurrence of large galictine mustelid, *Pannonictis*, from Asian part of former USSR (Table 5). Eight of mustelid specimens including six isolated tooth, left maxilla with P⁴, and right maxilla with P³ and P⁴, considered to be *Pannonictis*. *Pannonictis* differs from other Mustelidae in the sizes and shape of M₁ and P⁴, skull, and mandible. It is close to the South American extant genus *Grison* and to the extinct genus *Enhydriactis* from the Plio-Pleistocene of Europe (Sotnikova, 1980). The Middle Pleistocene East Asian *Oriensictis* is also close to *Pannonictis* (Ogino and Otsuka, 2008). The origin of *Pannonictis* is probably in Asia. Zdansky (1927) has described a large specimen of Mustelidae gen. et sp. indet. from the accumulations of late Miocene of China, which was similar to *Pannonictis*. Sotnikova (1980) considered that both of *Pannonictis* from the northern Mongolia (Shamar, MN 16a) and China (Gaotege, MN 15) are relatives of the Zdansky's mustelid. In Europe the oldest *Pannonictis* is known from the late Ruscinian of Hungary (Csarnota 1, MN 15) (García and Howell, 2008).

Subfamily Melinae Burmeister, 1850**Genus *Parameles* Rostshin, 1949*****Parameles suillus* (Teilhard et Leroy) 1945**

Kalmykov (1989) reported the occurrence of *Parameles suillus* from the Udunga fauna. Four left mandibles and isolated upper canine are considered to be *Parameles suillus* in the SSC Udunga collection (Table 6). Left mandible (Udg-0003) is described by Kalmykov (2003: p. 31, Fig.4). *P. suillus* (= *Meles suillus*), which has been described from adjournment of the sediments of Yushe (Teilhard de Chardin and Leroy, 1945), was found from Shamar (northern Mongolia) (Sotnikova, 1980). Several melid fossils have already been described under the different names from the early Pliocene Europe: *Parameles* from Odessa catacombs (Ukraine) and Weze (Poland) (Stach, 1951). According to Sotnikova and Kalmykov (1991), the priority belongs to *Parameles* Rostchin, so *Parameles* should include “*Meles*” *genevauxi* from Montopoli (France), *Arctomeles pliocaenicus* from Weze (Poland), *Parameles ferus* from the Odessa catacombs (Ukraine), *Meles suillus* from Yushe, Ertemte (China), Shamar (North

Table 7. Specimens of *Ferinestrix* sp. indet.

Udg-	side	Material	Udg-	side	Material
4	R	mandible with M ₁	167	R	mandible with lower canine and P ₂
6	L	mandible with P ₃ , P ₄ , and M ₂	168	R	mandible with M ₁
7	L	mandible with lower canine-M ₂	169		upper incisor
8	L	mandible with P ₃ -M ₁	170	L	mandible with P ₂ -M ₁
9	R	mandible with P ₃ -M ₁	171	R	mandible with P ₃ -M ₂
10	L	mandible with I ₂ , lower canine-M ₁	172	L	mandible with P ₄ -M ₂
11	L	mandible with P ₃	173	L	mandible with lower canine-M ₁
12	R	mandible with P ₃	174	R	mandible with P ₂ -M ₁
13	L	mandible with lower canine-M ₂	175	R	maxilla with P ³ -M ¹
14	L	mandible with P ₄ and M ₁	185	L	mandible with lower canine-M ₁
18	L	mandible with P ₂ and P ₄	1297	R	mandible with P ₄ and M ₁
19	L	maxilla with P ⁴	1302	L	upper canine
20	L	mandible with P ₄ -M ₁	1303	R	M ¹
31	L	mandible with P ₃ -M ₁	1304	L	P ³
32	L	mandible with m2	2005	R	lower canine
46	L	mandible with P ₄ -M ₂	2006	L	maxilla with P ³ and P ⁴
47	R	mandible with lower canine-M ₂	2007	L	mandible with M ₁
55	L	M ₁	2009	R	upper canine
56	R	M ₁	2010	L	upper canine
57		lower canine	2011	R	M ¹
68	L	M ₁	2012	R	M ₂
69	L	maxilla with P ³ and P ⁴	2013	L	M ₂
70	L	M ¹	2016	R	maxilla with M ¹
72	L	mandible with lower canine-M ₁	2017	R	maxilla with P ⁴ and M ¹
73	L	mandible with lower canine-M ₂	2018	L	maxilla with M ¹
74	L	mandible with M ₁ and M ₂	2031	R	mandible
75	R	maxilla with P ⁴ and M ¹	2005	L	lower canine
79	L	maxilla with P ⁴ and M ¹	2016	L	M ¹
82	L	mandible with P ₄ and M ₁	2017	R	M ¹
83	L	maxilla with P ⁴ and M ¹	2348		upper canine
89	R	mandible with lower canine-M ₁	2349		upper canine
90	L	M ¹	2352		upper canine
91	R	mandible with P ₄ and M ₁	2353		upper canine
111	R	mandible with M ₁	2459		upper canine
113	R	mandible with P ₄ and M ₁	2369		upper canine
114	L	mandible with M ₁	2370		upper canine
115	L	mandible with M ₁	2410		lower canine
116	L	mandible with P ₃ -M ₁	2411		lower canine
117	L	mandible with P ₃ -M ₁	2412		lower canine
122	R	M ¹	2413		lower canine
123	L	maxilla with P ³ and P ⁴	2415		upper canine
124	R	P ⁴	2416		upper canine
125	R	M ¹	2439		upper canine
130	R	maxilla with P ³	2431		upper canine
132	R	mandible with P ₃ -M ₁	2428		upper canine
133	R	mandible with lower canine, P ₃ , P ₄	2429		upper canine
135	R	maxilla with P ⁴ and M ¹	2424		lower canine
136	L	M ¹	2425		lower canine
137	L	maxilla with P ⁴ and M ¹	2426		lower canine
141	L	maxilla with P ⁴	2454		lower canine
158	R	maxilla with P ³ and P ⁴	2455		lower canine
159	L	maxilla with P ³ - M ¹	2472		upper canine
164	L	maxilla with M ¹	2408	R	M ₁
165	R	maxilla with P ⁴ and M ¹			

Mongolia) and Udunga. Thus, the stratigraphical range of *P. suillus* is considered from the end of Turolian (MN 13) to the beginning of early Villafranchian (MN 16a) (Li *et al.*, 1984; Wolsan, 1989; Sotnikova, Kalmykov, 1991; Kalmykov, 1992; Tedford, 1995; Vangengeim *et al.*, 1998).

Table 8. Specimens of *Parailurus baikalicus*.

Udg-	side	Material
1	R	mandible with lower canine-M ₂
51	R	M ₂
52	R	M ₁

Genus *Ferinestrix* Bjork, 1970***Ferinestrix* sp. indet.**

An enigmatic form of large badger is identified as *Ferinestrix* sp. by Sotnikova (2006). Formerly a large badger was defined as Mustelidae gen. nov. et sp. nov (Kalmykov, 1989). The most abundant carnivore in the SSC Udunga collection is *Ferinestrix* (Table 7), which was only known from the Pliocene North American Hagerman local fauna and established on the basis of the fragment of mandible with incomplete M₁ (Bjork, 1970).

Family Ailuridae Gray, 1843**Genus *Parailurus* Schlosser, 1899*****Parailurus baikalicus* Sotnikova, 2008**

Only three specimens are available to us (Table 8). Right mandible with complete cheek teeth row (Udg-0001) has been reported by Kalmykov (2002: p. 211, Fig. 3). All dentition of Udg-0001 are considerably worn, indicating that it belong to an old individual, while two isolated teeth, right M₁ (Udg-0052) and M₂ (Udg-0051), have weak dental attrition.

These ailurid specimens are considered to belong to the large lesser panda, *Parailurus baikalicus* Sotnikova, 2008 from Udunga. Although extant lesser panda, *Ailurus fulgens* is limited to the Himalayan highland forest, the extinct large lesser panda *Parailurus* is widely distributed in the Pliocene northern hemisphere including Europe, Asia, and North America (Kundrát, 1997; Morlo and Kundrát, 2001; Sasagawa *et al.*, 2003; Wallace and Wang, 2004; Sotnikova, 2008). Several specimens of Ailuridae are known from the Udunga fauna and numerous lists of fauna was specified as *Ailurus* sp. (Kalmykov, 1999, 2003, Erbajeva *et al.*, 2003; Kalmykov, Maschenko, 2005, 2006; Kalmykov *et al.*, 2005; Maschenko *et al.*, 2007). Erbajeva *et al.* (2003) identified these specimens to *Parailurus* sp., but later it was redescribed as *Parailurus baikalicus* (Sotnikova, 2008) on the basis of the fragment left maxilla (No. 962/58, БФ ГИИ) with P⁴, M¹⁻² and the alveolus of the distal root of P³. The Transbaikalian *P. baikalicus* is larger than the European *P. anglicus*, but likely corresponds to *P. hungaricus*. *Parailurus* sp. from the Pliocene Japan (Sasagawa *et al.*, 2003) differs from *P. baikalicus* by having primitive characteristics on P⁴.

Table 9. Specimens of *Pliocrocute* sp. indet.

Udg-	side	Material	Udg-	side	Material
24	R	mandible with P ₂ -M ₁	187	L	maxilla with P ³ and P ⁴
25	R	mandible with lower canine, P ₄ , M ₁	188	L	maxilla with P ² -P ⁴
26	R	mandible with lower canine-M ₁	1301	L	I ₁ -I ₃
27	L	mandible with P ₂ -M ₁	2008	L	P ³
29	R	mandible with lower canine-M ₁	2014	R	M ₁
30	L	mandible with M ₁	2015	R	mandible
41	R	mandible with P ₂ -M ₁	2019	R	mandible
71	R	mandible with lower canine-M ₁	2020		lower incisor
100	L	P ⁴	2021	R	I ₃
156	R	mandible with P ₃ and P ₄	2022	L	I ₃
180	R	mandible with P ₂ -M ₁	2028	R	mandible with P ₃ -M ₁
181	R	mandible with P ₃ -M ₁	2032	R	M ₁
182	L	mandible with lower canine-M ₁	2033	L	P ₃
183	R	mandible with lower canine-M ₁	2034	L	P ₄
186	R	maxilla with P ³ and P ⁴	2035	L	M ₁

Family Hyaenidae Gray, 1869**Genus *Pliocrocute* Koretzoï, 1938*****Pliocrocute pyrenaica* (Deperet), 1890**

30 specimens are considered to be *Pliocrocute pyrenaica* (Table 9). Right mandible (Udg-0026) of *P. pyrenaica* has been reported by Kalmykov (2003: p. 32, Fig.5). *P. pyrenaica* retains primitive morphological feature and similar to the late Ruscinian or the earliest Villafranchian hyaenid form (Kalmykov, 1992; Sotnikova, 2006). The identification of *Pliocrocute* is constructed based on tooth morphology. The characteristics of M₁ differs from that of *Hyaena*. The length of P₄ is much greater than that of *Ictitherium* (Sotnikova, 1989). *Pliocrocute* possibly includes fossil hyenids from Layna (*Hyaena pyrenaica*), Odessa catacombs (*Crocute* cf. *sivalensis*), Beregovaya (*Crocute* cf. *licenti*), Kuruksai (*Pachycrocute* cf. *perrieri*), Leijiahe (*Hyaena licenti*) (Kalmykov, personal communication). *P. pyrenaica* is common not only in Udunga but also in the early Pliocene of Europe, such as Serrat den Vocquer (France), Layna (Spain), and Odessa catacombs (Ukraine). *Pliocrocute* is distributed in the wide area of northern Eurasian continent from Spain to the Baikal lake in the early Pliocene (Vangengeim *et al.*, 1998). In the Pliocene of Europe some stages of the development of the genus from *P. pyrenaica* of Ruscinian to the derived form, *P. perrieri* (Sotnikova, 1989). In Central Asia *Pliocrocute* is known from the early to middle Pleistocene. Kurten (1956) marked finds of two large forms such as *P. brevirostris licenti* and *P. brevirostris sinensis* in Zhoukoudian, northern China. Subspecies of *P. brevirostris* is also known from Transbaikalia (Zasukhina, Tologoi) and from the Northern Mongolia (Nalaiha) (Vislobokova *et al.*, 1995). *P. perrieri* is reported from the late Pliocene localities in Asia, such as Youhe (China) and Kuruksay (southern Tajikistan) (Howell, Petter, 1980; Sotnikova, 1989). In Asia, *Pachycrocute pyrenaica orientalis* is known from the Villafranchian China (Qiu, 1987). Unfortunately, the Chinese material on hyaenid is not stratified, therefore new data on *P. pyrenaica* from the western Transbaikalia area would be

Table 10. Specimens of *Chasmaporthetes* sp. indet.

Udg-	side	Material
45	L	mandible with P ₂ -M ₁
184	L	mandible with P ₂ -M ₁

Table 11. Specimens of *Lynx shansius*.

Udg-	side	Material	Udg-	side	Material
15	R	mandible with lower canine-M ₁	127	R	maxilla with P ³ and P ⁴
22	R	mandible with lower canine-M ₁	134	R	mandible with P ₃ and P ₄
33	L	mandible with lower canine, P ₄ , M ₁	138	L	mandible with lower canine, P ₃ , P ₄
34	R	mandible with lower canine, P ₄ , M ₁	139	R	mandible with P ₄ and M ₁
35	R	mandible with lower canine-M ₁	157	L	mandible with I ₃ and P ₃
36	R	mandible with lower canine-M ₁	160	R	mandible with lower canine-M ₁
38	R	mandible with P ₃ -M ₁	166	L	maxilla with P ⁴ and M ¹
39	L	mandible with P ₃ -M ₁	179	L	mandible with lower canine-P ₄
40	L	mandible with lower canine-M ₁	1295	L	mandible with P ₃ -M ₁
44	L	mandible with P ₃ -M ₁	1305		lower canine
77	R	maxilla with P ³ and P ⁴	1306		lower canine
86	R	mandible with lower canine-M ₁	1307		lower canine
110	R	mandible with P ₃ -M ₁	1308	R	mandible with lower canine and P ₃
118	L	mandible with P ₃ and P ₄	1309	R	P ₄

important for the study of its dispersal and evolution.

Genus *Chasmaporthetes* Hay, 1921

Chasmaporthetes sp. indet.

Vislobokova *et al.* (2001) reported the occurrence of a gracile hunting hyaena, *Chasmaporthetes*, from Asian part of the former USSR. Only two left mandibles with P₂-M₁ considered to be this genus (Table 10). *Chasmaporthetes* was widely distributed in the Plio-Pleistocene northern hemisphere including North Africa, Europe, Asia, and North America (e.g. Hay, 1921). In Asia *Chasmaporthetes* (*C. lunensis*) is discovered from the late Pliocene of the Northern Mongolia (Shamar) and Udunga. The fossil specimens of the hunting hyaena are discovered in western Transbaikalia area (Beregovaya) and Tajikistan (Kuruskay), and have been described as *Euryboas* (Sotnikova, 1974, 1976, Vangengeim *et al.*, 1988). Repenning (1967) has proposed an assumption that *Euryboas* is a synonym of genus *Chasmaporthetes*. Savage and Curtis (1970) and Kurtén and Werdelin (1988) supported his opinion. However, the priority of the genus *Chasmaporthetes* has been restored even later (Kurten and Crusafont, 1977). According to Sotnikova (1994), *Chasmaporthetes* includes *C. borissiakii* (presumably late Miocene, Moldova), *C. exitelus* (late Miocene, China), *C. lunensis* (Pliocene - early Pleistocene, Eurasia), *C. ossifragus* (late Pliocene - early Pleistocene, North America), *C. nitidula* (late Pliocene - early Pleistocene, Africa). Thus, chronological distribution of *Chasmaporthetes* is from the late Miocene to the early Pleistocene.

Table 12. Specimens of *Homotherium* sp. indet.

Udg-	side	Material
21	R	mandible with lower canine, P ₄ , M ₁
23	R	mandible with P ₄ and M ₁
76	R	P ⁴
101	R	P ⁴

Family Felidae Gray, 1821**Genus *Lynx* Kerr, 1792*****Lynx shansius* Teilhard et Leroy, 1945**

Kalmykov (1989) reported the occurrence of *Lynx shansius* from the Udunga locality. 28 specimens are considered to be this species in the SSC Udunga collection (Table 11) and a right mandible (Udg-0160) has been described by Kalmykov (2003: p. 34, Fig. 6). *Lynx* from Udunga is known to be one of the oldest lynxes: its morphology is more primitive than that of *Lynx shansius* from the Shamar and Yushe and *L. issiodorensis* from Pardines (France) and Val d'Arno (Italy) (Kurten and Werdelin, 1984). *Lynx* appeared in the late Ruscinian and is known from Moldova and Odessa catacombs (Vangengeim *et al.*, 1998).

Genus *Homotherium* Fabrini, 1890***Homotherium* sp. indet.**

Kalmykov (1989) firstly reported the occurrence of *Homotherium* sp. from the Udunga locality. Two right mandibles and two isolated right P⁴ are considered to be *Homotherium* in the SSC Udunga collection (Table 12). *Homotherium* is considered to have separated from *Machairodus* at the end Miocene (Anton and Galobart, 1999), but *H. crenatidens* is known from the Villafranchian of Eurasia (Bajgusheva, 2000; Hemmer, 2001; Sotnikova *et al.*, 2002). The saber-toothed cat, Machairodontinae, is discovered from the Ruscinian locality of Europe and Asia, but the materials are so fragmentary to define their essential characteristics (Vekua, 1972; Perez, Soria, 1989-1990). *Homotherium* sp. from the Ruscinian Odessa catacombs (Ukraine), differs from the Villafranchian specimen in its primitive characteristics (Vangengeim *et al.*, 1998).

Discussion

Eleven genera of carnivores have been recognized from the SSC Udunga collection (Table 1). The Udunga fauna is recognized as the end of early Pliocene (Kalmykov, 1989, 1992, 2003; Sotnikova and Kalmykov, 1991; Kalmykov and Malaeva, 1994; Kalmykov and Maschenko, 2005, 2006; Kalmykov *et al.*, 2005; Maschenko *et al.*, 2007; Maschenko *et al.*, 2007) or the early Late Pliocene (MN 16a, Vislobokova *et al.*, 1993; Vislobokova *et al.*, 1995; Erbajeva *et al.*, 2003) on the basis of biostratigraphical study of many kind of mammals.

However, the Pliocene Eurasian carnivores were widely distributed spatiotemporally, and carnivore taxa of the Udunga fauna have close relationships not only to the Eurasian but also to the African and North American assemblages.

Vislobokova *et al.* (1995) referred that the occurrence of *Parameles suillus* and *Ursus minimus* from the Udunga fauna indicates analogues with Beregovaya assemblage (MN 16b; Transbaikal, Russia) and Shamar assemblage (2.8 Ma; Mongolia). The former carnivoran assemblage is represented by *Nyctereutes sinensis*, *Eucyon cf. minimus*, *Chasmaporthetes lunensis*, *Lynx shansius* and *Acinonyx cf. pardinensis* (Alexeeva and Erbajeva, 2006). The latter carnivoran assemblage is represented by *Nyctereutes megamostoides*, *Mustela* sp., *Pannonictis pachygnata*, *Meles (=Parameles) suillis*, *Hyaena cf. licenti*, *Euriboas cf. lunensis*, *Felis (=Lynx) shansius*, and *Acinonyx* sp. (Sotnikova, 1980 and Zazhigin, 1989). Vislobokova *et al.* (1995) also pointed out that *Ursus minimus*, *Pachycrocuta (=Pliocrocuta) pyrenaica*, and felids are comparable to the Italian Triversa fauna (MN 16a; Azzaroli *et al.*, 1988). The Khapry faunal assemblage reported from the coastal zone of Azov Sea, Russia, (MN 17) was recently revised by Sotnikova *et al.* (2002), where the carnivoran assemblage is represented by *Nyctereutes megamostoides*, *Canis cf. senecensis*, *Lutra* sp., *Pannonictis nesti*, *Pliocrocuta perrieri*, *Pachycrocuta brevirostris*, *Homotherium crenatidens*, *Acinonyx pardinensis*, and *Lynx issiodorensis*. Sotnikova (2008) referred that the similarity of *Pliocrocuta* and *Parameles* from the Udunga fauna to corresponding forms from the fauna of Odessa Catacombs, Ukraine (terminal Ruscinian).

Qiu and Qiu (1995) summarized the Chinese Neogene mammalian faunas and described the two Pliocene faunas from Shanxi Province. In the Yushe basin, *Pliohyaena (=Pliocrocuta) pyrenaica*, *Chasmaporthetes*, and *Nyctereutes* have been discovered from Gaozhuang fauna with a paleomagnetic age of 5.2 - 3.4 Ma. Deng *et al.* (2004) reported the Early Pliocene (MN14 - MN15) Hewangjia mammalian assemblage, Gansu Province, which includes three carnivoran genera, *Promephitis* sp., *Chasmaporthetes* sp., and *Hyaenictitherium wongi*, while *Ursus*, *Nyctereutes*, and *Canis* have not been found there. The absence of these forestal elements indicates that the sedimentary paleoenvironment of the Hewangjia fauna was dry condition.

Ursus, *Parameles*, and *Pliocrocuta* of the Udunga fauna show primitive features (Sotnikova, 2006) and these taxon borrow(???) heavily from the Ruscinian form. *Chasmaporthetes*, *Parailurus*, *Gulo*, and felids are discovered across the Northern Hemisphere including Europe, Asia, North Africa, and North America. The enigmatic large badger, *Ferinstrix*, was only known from the Pliocene North American Hagerman local fauna (Bjork, 1970). As mentioned above, carnivores of the Udunga fauna are considerable to the evidence of active exchanges between the New World and Old World in the Pliocene and this fauna is important for discussing about mammalian dispersal event in the Northern Hemisphere at the period. In addition, this fact shows the difficulty to use carnivore to the biostratigraphical study.

On the other hand, feeding habitat of carnivore is clearly discriminated from the fossil materials and it is useful to reconstruct the paleoenvironment. The abundance of animals of thermophilic forest biotopes and their unusual composition (with *Ursus*, *Parailurus*, *Parameles*, and *Ferienstrix*) is peculiar feature of carnivores of the Udunga fauna (Sotnikova, 2006). However, *Hipparion* (*H. houfenense* and *H. tchicoicum*), *Dicerorhinus*, bovids, and *Chasmaporthetes* are representative of the open land elements. The occurrence of both forestal and semiarid mammals indicates that the Udunga fauna is comprised of mosaic elements.

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