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# Carnivores of the Khapry Faunal Assemblage and Their Stratigraphic Implications

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**Abstract**—Carnivores of the Khapry faunal assemblage that is commonly considered as an analogue of the middle Villafranchian West European fauna (Late Pliocene, Zone MN17) were revised. Members of nine Carnivora genera are described in detail, and five of them are first included in the list of assemblage taxa. Carnivores of the Khapry assemblage are represented by *Nyctereutes megamastoides* (Pomel), *Canis* cf. *senezensis* Martin, *Lutra* sp., *Pannonictis nestii* (Martelli), *Pliocrocuta perrieri* (Croizet et Jobert), *Pachycrocuta brevirostris* (Aumard), *Homotherium crenatidens* (Fabrini), *Acinonyx pardinensis* (Croizet et Jobert), and *Lynx issiodorensis* (Croizet et Jobert). The Khapry carnivore assemblage includes taxa characteristic of the Late Pliocene Eurasian faunas. Its lower stratigraphic limit corresponds to the beginning of the middle Villafranchian, as it follows from presence of *Homotherium crenatidens* with more advanced dental characteristics than those of homotheres from the lower Villafranchian of Eurasia. The occurrence of *Nyctereutes megamastoides* that was not encountered above the middle Villafranchian bounds the upper stratigraphic limit of the Khapry Carnivora. The "*Canis*-event" and "*Pachycrocuta*-event" are considered to be important records around the middle-upper Villafranchian boundary in Europe. Presence of *Canis senezensis* is characteristic of the final stage of the middle Villafranchian in Western Europe, and dispersal of *Pachycrocuta brevirostris* is typical of the lowermost late Villafranchian, whereas the wolflike forms of *Canis* and *Pachycrocuta* appeared somewhat earlier in Asia. The Khapry faunal assemblage as a whole is characterized by a certain similarity with Asian analogues of the middle Villafranchian faunas.

**Key words:** Pliocene, Villafranchian, Khapry faunal assemblage, Russia, Azov region, Carnivora, morphology, stratigraphy, correlation.

## INTRODUCTION

The Khapry sand–shingle deposits yielding mammal faunal remains are widespread in the coastal zone of the Sea of Azov between the Rostov-on-Don and Taganrog. They unconformably overlie the marine Miocene sediments and correspond to alluvium of an ancient 30 to 40-m terrace of the Don River.

Since 1932, the remains of large mammals from the Khapry sequence were collected in four sites, namely, in the Khapry and Liventsovka quarries in the Rostov-on-Don area and in the Morskaya and Volovaya Balka localities near Taganrog (Fig. 1). In all mentioned sites, fossil remains are mainly confined to the lower part of the alluvial sequence, however, separate bones occur in the higher parts of the Liventsovka section as well.

Based on geologic and taphonomic observations and according to paleontological records, many researchers inferred that remains of large mammals accumulated in the Khapry sequence during the formation of a single sedimentary cycle. The remains were defined by Gromov (1948) as the Khapry Faunal Unit of the late Pliocene age.

The most comprehensive information on large mammals from the Liventsovka locality is represented in papers of Baigusheva (1971, 1994) and monograph by Alekseeva (1977) summarizes data on the whole Khapry assemblage.

The Khapry faunal assemblage is dominated by remains of *Archidiskodon gromovi* (Garutt et Alexeeva) and large horses of the *stenonis* group. Based on large mammals, it is correlated with the middle Villafranchian faunas of Central and Western Europe (Alekseeva, 1977; Vangengeim and Zazhigin, 1982). In the Liventsovka locality however, several beds rich in small mammal bones were distinguished in the 20-m-thick alluvial deposits of the Khapry sequence. The lower beds bearing megafauna yield a rodent assemblage corresponding to the lower part of the Zone MN17 of the middle Villafranchian. The Liventsovka microtheriofauna as a whole falls into a wide time span within the pre-Olduvai portion of the Matuyama Chron (Tesakov, 1995).

The Perissodactyla and Artiodactyla from the Khapry faunal assemblage were described and repeatedly discussed in the literature, whereas Carnivora were

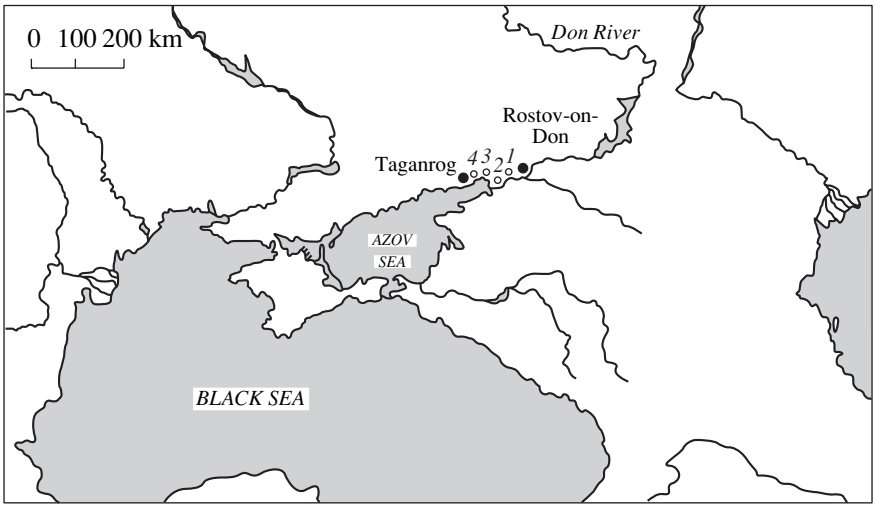


**Fig. 1.** Localities of carnivores of the Khapry faunal assemblage: (*1*) Liventsovka; (*2*) Khapry; (*3*) Morskaya; (*4*) Volovaya Balka.

listed only with a brief information on their findings. According to Gromov (1948), Baigusheva (1971), and Alekseeva (1977), the initial summary list of carnivores from the Khapry sands included *Canis* sp., *Nyctereutes megamastoides* (Pomel), Mustelidae gen., *Meles* sp., *Lutra* sp., *Ursus* cf. *etruscus* Cuv., *Crocuta* sp., *Machairodus* sp., *Lynx* sp., and Felidae gen. (large form). Judging from the list, carnivores from the Khapry alluvium are heterochronous taxa: *Machairodus* is the Miocene form, *Nyctereutes megamastoides* is a Pliocene species, and *Crocuta* represents the Pleistocene animals. The revision and thorough description of carnivores of the Khapry faunal assemblage is undoubtedly desirable, and the results obtained are presented in this work.

The carnivore remains described below have been collected from the Liventsovka, Khapry, Morskaya, and Volovaya Balka localities (Table 1). They are stored at the Rostov-on-Don Regional Museum, Azov Museum of Regional Studies, Geological Institute RAS (GIN), and at the Vernadsky State Geological Museum (VSGM) in Moscow. The original *Canis* mandibles from the Khapry locality are lost, and their casts from the VSGM are described here. The *Ursus* specimens are now missing from the collection.

When correlating the Khapry carnivore assemblage with the European analogues, we used subdivisions of the West European continental scale, namely, the Ruscinian, Villafranchian, and Gallerian stages and the "Faunal Units" Saint-Vallier, Costa San Giacomo (= "Séneze Faunal Unit" in Rook and Torre, 1996), Olivola, and Tasso of the Villafranchian. In the Italian stratigraphic scale, the late Villafranchian begins with the Olivola Faunal Unit. According to paleomagnetic records, the Olivola fauna corresponds to the uppermost Olduvai Subchron, and the Costa San Giacomo Unit is correlated with the pre-Olduvai portion of the Matuyama Chron (Torre *et al.*, 1993; Sardella *et al.*, 1998).

The abbreviations used in the text and tables indicate institutions, collections, and measurements.[1]

## SYSTEMATIC PALEONTOLOGY

Order Carnivora Bowdich, 1821

Family Canidae Gray, 1821

Genus *Nyctereutes* Temmnick, 1838

*Nyctereutes megamastoides* (Pomel, 1842)

Plate I, figs. 1 and 2

*Nyctereutes megamastoides*: Alekseeva, 1977, Plate 1, figs. 5 and 6.

*Material*: left ramus with a well preserved ascending ramus; i1–p3 are missing, m3 is represented by alveolus, talonid cusplets of m1 and m2 are worn; GIN 302/1.

*Locality*: Volovaya Balka, the Khapry sequence.

*Description and comparison. Nyctereutes* from the Khapry alluvium differs from *N. donnezani* (Depéret) and *N. tingii* Tedford et Qiu by a well developed digastric process on the mandible. This feature makes it similar to the more advanced Villafranchian species *N. megamastoides* and *N. sinensis* (Schlosser) from Eurasia. The described specimen is one of the biggest

[1] (RAS) Russian Academy of Sciences; (GIN) Geological Institute RAS, Moscow; (PIN) Paleontological Institute RAS, Moscow; (VSGM) Vernadsky State Geological Museum RAS, Moscow; (RSU) Rostov State University, Rostov-on-Don; (RRM) Rostov Regional Museum, Rostov-on-Don; (AMNH) American Museum of Natural History, New York; (F:AM) Frick Collection in the AMNH; (QSV) Saint-Vallier Collection, Museum of Natural History, Lyons; (IGF) Museum of Geology and Paleontology, Florence; (OSU) Odessa State University, Odessa; (KPM) Kiev Paleontological Museum; (L) length; (W) width; (D) depth; (H) height; (T) thickness; (al) alveolus; (LMt) metastyle length; (Md) mean dimensions. All measurements are given in mm.

among known fossil racoon dogs. Its mandible height in the coronoid process, H = 64.5; the mandible deepness behind m1, D = 21.5; the length from m1 to the mandibular condyle, L = 72.5. The distance between the m2 posterior margin and the angular process in specimen GIN 302/1 is 49.5, whereas in the *N. megamastoides* population from Saint-Vallier this distance ranges from 37.0 to 44.0 (Martin, 1971). The dimensions of m1 in the Khapry *Nyctereutes* are close to those of the Asian Pliocene analogues, and the European forms are smaller on the average (Fig. 2).

The angular process of the discussed specimen is enlarged and lacks a dorsal hook as in *N. megamastoides* and *N. sinensis.* In the late Pleistocene *Nyctereutes* sp. from Choukoutien-1 and living *N. procyonoides* (Gray), the process is still more expanded. At the medial side of the angular process, the dorsal fossa for the superior ramus of the medial pterygoid muscle is distinctly larger than the ventral fossa for the inferior ramus of the muscle. This structure of the interior area of the angular process contrasts with that of *N. procyonoides*, in which ventral fossa is larger than the dorsal one. The relationship of size of the muscle fossae in *Nyctereutes* from the Khapry faunal assemblage (Fig. 3) differs from that of *N. sinensis* from the Mazegou Formation (Tedford and Qiu, 1991) and agrees with the angular area morphology of *N. megamastoides* from Saint-Vallier site (Martin, 1971).

Like other racoon dogs, *Nyctereutes* from the Khapry sequence has a low-crowned p4 without accessory cusplets. There is no posterior expansion of the crown as seen in the early Pliocene *N. donnezani* from Wże (Czyżewska, 1969, fig. 3, p. 446). The m1 has a relatively large hypoconulid shelf and the metastylid is absent. The worn m2 most likely had a paraconid and a simple talonid.

The teeth measurements are L/W p4 = 11.4/5.0; L/W m1 = 18.4/7.6; L/W m2 = 9.2/7.2.

*Discussion.* The late Pliocene *N. megamastoides* from Eurasia and *N. sinensis* from China are closely allied morphologically and are often considered as geographical varieties of a single taxon (Viret, 1954; Soria and Aguirre, 1976; Tedford and Qiu, 1991). On the average, the Asian *Nyctereutes* specimens are larger than the European ones, however, this is likely a feature of the population characteristics rather than indication of the geographical variability. For instance, the racoon dogs from Shamar (Mongolia) and Kvabebi (Georgia) are commeasurable with their European counterparts from the Villarroya, Saint-Vallier, and Puebla de Valverde sites, whereas the Khapry *Nyctereutes* represents a very large specimen comparable with those from Tajikistan, Transbaikal region, and the Nihewan locality of China (see Fig. 2).

Variations in the structure of the interior side of the angular process in the fossil *Nyctereutes* are imperfectly understood as yet, though this character is of great importance in the phylogenetic reconstruction of

**Table 1.** Distribution of carnivores of the Khapry faunal assemblage in studied localities

| Taxa | Liventsovka | Khapry | Morskaya | Volovaya Balka |
|---|---|---|---|---|
| *Nyctereutes megamastoides* | | | | × |
| *Canis* cf. *senezensis* | × | × | | |
| *Lutra* sp. | × | | | |
| *Pannonictis nestii* | × | | | |
| *Pliocrocuta perrieri* | × | × | ? | |
| *Pachycrocuta brevirostris* | × | | | |
| *Lynx issiodorensis* | × | | | |
| *Acinonyx pardinensis* | × | | × | |
| *Homotherium crenatidens* | × | | | |

Caninae. The enlarged angular process with an expanded inferior pterygoid fossa is evaluated as an advanced character among living Caninae (Tedford *et al.*, 1995). The expanded inferior pterygoid fossa is seen in *N. sinensis* from the Liujiagou locality of China (refer to Fig. 3) and in the Pleistocene *Nyctereutes* sp. from the Choukoutien site, and is characteristic of the living *N. procyonoides.* Plesiomorphic features of the angular process structure are evidenced in the more primitive Eurasian racoon dogs *N. tingii* and *N. donnezani* characterized by not expanded angular process and

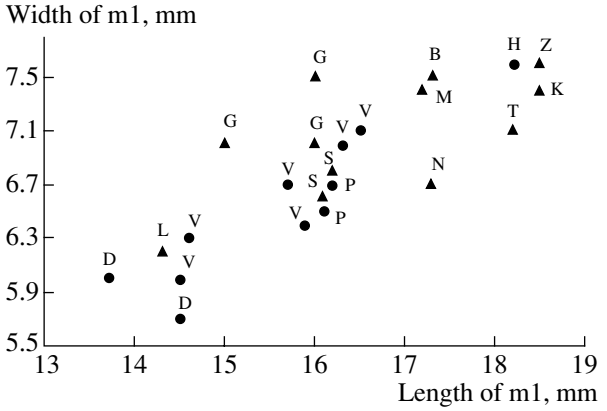


**Fig. 2.** The length/width ratio for lower m1 of *Nyctereutes megamastoides* and *N. sinensis* from the late Pliocene localities of Eurasia. Europe: (H) Volovaya Balka, GIN 302/1; (D) Dafnero (Koufos and Kostopoulos, 1997); (P) Puebla de Valverde (Kurtén and Crusafont, 1977); (V) Villarroya (Soria and Aguirre, 1976). Asia: (G) Kvabebi (Vekua, 1972); (K) Kuruksai (Sharapov, 1981); (Z) Zilfi; (T) Tutak, collection of GIN; (B) Beregovaya, collection of GIN; (S) Shamar; (M) Dzagkso-Hairhan 3, collection of GIN; (L) Liujiagou (Tedford and Qiu, 1991, fig. 1); (N) Nihewan (Teilhard de Chardin and Piveteau, 1930); circles for European and triangles for Asian localities.

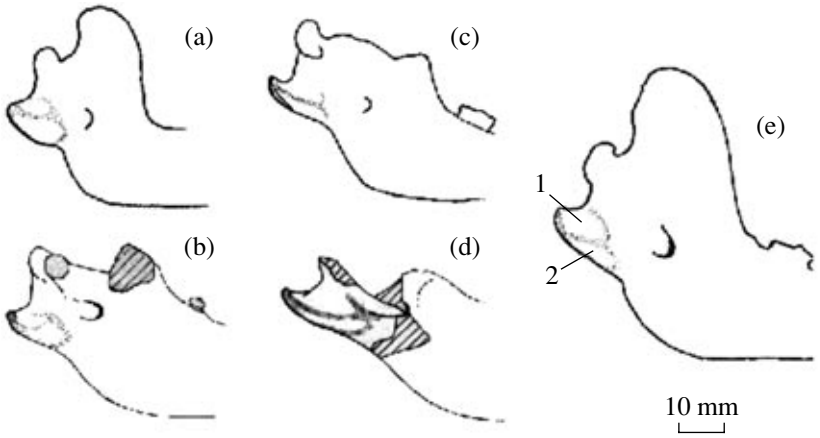


**Fig. 3.** Position of fossae for pterygoid muscle attachment at the medial side of the mandibular angular process in some *Nyctereutes*: (a) *N. procyonoides*, collection of the Moscow State University Zoological Museum; (b) *N. sinensis*, Liujiagou, Mazegou Formation, China, F:AM 97007 (Tedford and Qiu, 1991); (c) *N. megamastoides*, Saint-Vallier, France, QSV-100 (Martin, 1971); (d) *N. tingii*, Liujiagou, Mazegou Formation, China, F:AM 97029 (Tedford and Qiu, 1991); (e) *N. megamastoides*, Volovaya Balka, Azov region, GIN 302/1; (1) upper pterygoid fossa; (2) lower pterygoid fossa.

fossa for the inferior branch of the medial pterygoid muscle (Tedford and Qiu, 1991). According to this character, *N. megamastoides* from the Khapry sands and *N. megamastoides* from the Saint-Vallier (QSV-100) are more advanced than *N. donnezani* and *N. tingii* and look more primitive than *N. sinensis* (specimen F:AM 97007) and *N. procyonoides.*

Genus *Canis* Linnaeus, 1758

*Canis* cf. *senezensis* Martin, 1973

Plate I, figs. 3–7

*Canis?*: Gromov, 1948, p. 45;

*Canis* sp.: Baigusheva, 1971, p. 11; Alekseeva, 1977, pp. 75–76.

*Material*: fragment of a left maxilla with incomplete p4 and m1-2, RSU-778; fragment of a right ramus with broken p4 and m1-2, VSGM-1 cast; fragment of a left ramus with m1-2, VSGM-2 cast.

*Localities*: Liventsovka, RSU-778; Khapry, VSGM-1, VSGM-2; the Khapry sequence.

*Description and comparison.* The length of the upper carnassial of *Canis* from the Khapry alluvium, L = 19.0 al., is less than in *C. etruscus* Forsyth Major, L = 21.3–24.0,[2] and close to that of *C. senezensis* Martin, L = 19.0–19.2; it lies within the range of *C. arnensis* Del Campana, L = 17.8–22.9. P4 of the RSU-778 is relatively narrow, with a long metastyle LMt = 7.2. The buccal and anterolingual cingula of M1 are well developed, the paracone and metacone are relatively low–crowned, and a shallow protocone and well–developed hypocone basins occur. According to the length of M1 (L = 12.6), *Canis* from Liventsovka is smaller than *C. etruscus* with M1L = 13.2–16.5 and corresponds to *C. senezensis* (M1L = 12.2) and *C. arnensis* (M1L = 11.7–15.3). M2 with L/W = 6.8/10.3, has a strong buccal cingulum and its proportions are similar to those of *C. senezensis* and *C. arnensis.*

The lower carnassial of the Khapry wolf has a wide and short talonid with a small talonid basin closed posteriorly by a hypoconid and large entoconid. The hypoconulid shelf on m1 is hardly visible in specimen VSGM-1 and almost missing on m1 in the second specimen. The large m2 has a big paraconid basin and a relatively wide talonid. Measurements of the lower molars, m1L = 22.4 and 23.2, m1W = 8.0 and 9.0, m2L = 9.7 and 10.2, m2W = 6.3 and 7.4, are close to those of *C. arnensis* (m1L = 20.3–23.7; Md = 21.9) and are on the average slightly less than in *C. etruscus* (m1L = 22.9–26.0; Md = 24.6). The Khapry form is distinguishable from *C. etruscus* and *C. arnensis* in the following characters: its hypoconulid shelf on the talonid of m1 is poorly developed, the entoconid is large and closely pressed at the base to the hypoconulid that is responsible for the posterior closure of the talonid basin. The same structure of m1 is seen in the primitive *Canis* cf. *etruscus* from the Kuruksai fauna of southern Tajikistan, which has a short and wide talonid with a large entoconid and talonid basin well closed posteriorly and lacking a hypoconulid shelf. At the same time, *Canis* from the Khapry alluvium differs from the Kuruksai form by the following features: the protocone of P4 is less anteriorly protruded, the upper molars are narrower relative to their length, the talonid cusps (hypoconid and entoconid) on m1 are less closely set at the base, m2 is shorter. The comparison of the upper teeth shows that the Khapry canid is close to *C. senezensis* in both the size and presence of relatively short P4 and M1 and of low paracone and metacone on M1.

*Discussion.* The medium-sized pre-Quaternary *Canis* s. str. are scarce and poorly studied in Eurasia.

[2] Measurements of *C. etruscus, C. arnensis*, and *C. senezensis* are given according to Rook (1993).

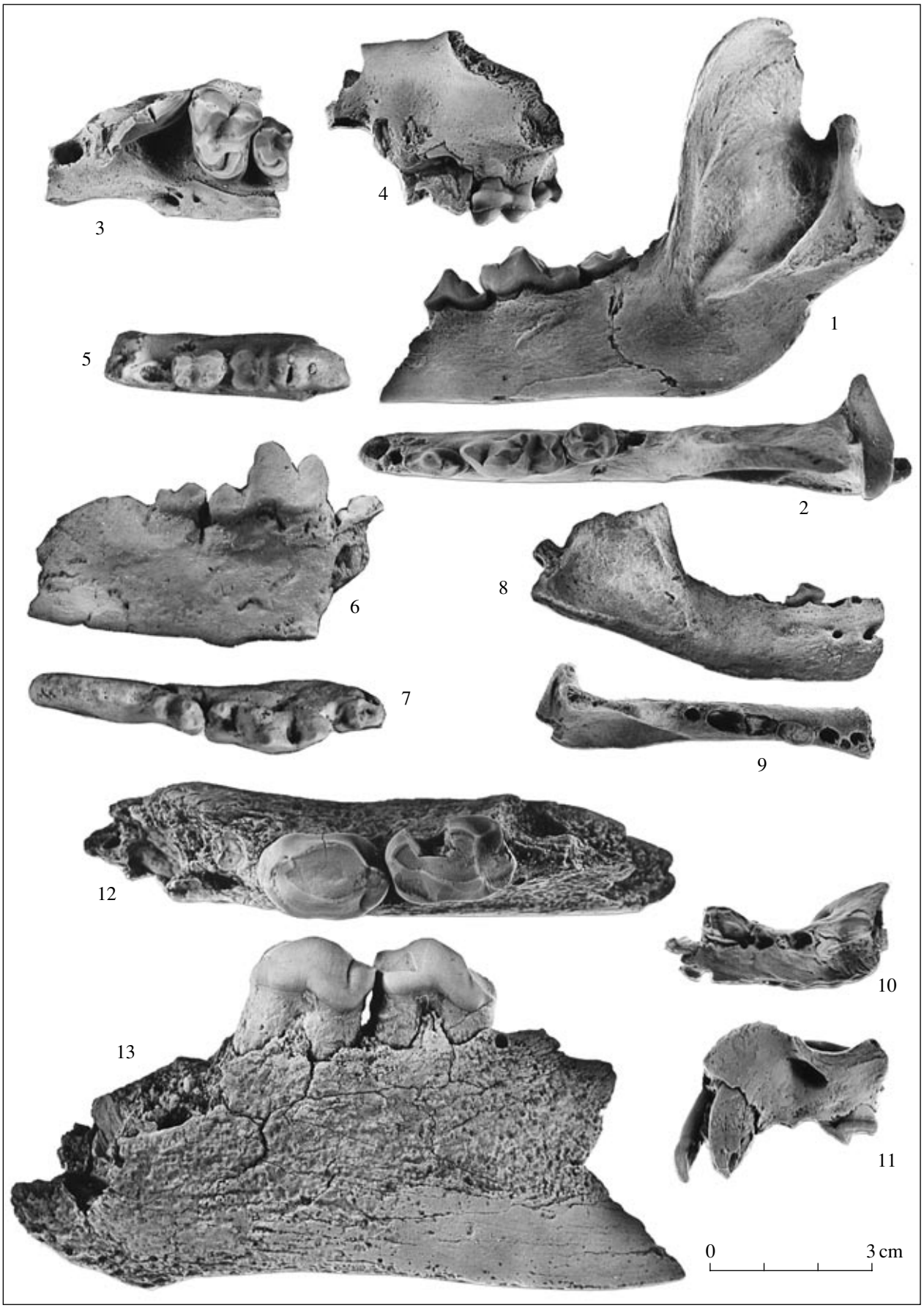
3
4
1
5
2
6
8
7
9
12
10
13
11
0
3 cm

**Plate I.** Carnivores of the Khapry faunal assemblage.

*Nyctereutes megamastoides*, left ramus, GIN 302/1: (1) lateral and (2) occlusal views. *Canis* cf. *senezensis*, fragment of left maxilla with p4–m2, RSU-778: (3) occlusal and (4) lateral views; fragment of left ramus with m1-2, VSGM-2, cast: (5) occlusal view; fragment of the right ramus with p4–m2, VSGM-1, cast: (6) lateral and (7) occlusal views. *Pannonictis nestii*, right ramus with p4, RSU-98: (8) lateral and (9) occlusal views; fragment of the left anterior part of the skull with I3, C1, and P4, RSU-1327: (10) occlusal and (11) lateral views. *Pliocrocuta perrieri*, mandibular fragment with p1–p2, RSU-1512: (12) occlusal and (13) lateral views (scale: 1 × 1).

The oldest primitive *C.* cf. *etruscus* was found in the Mazegou Formation of China that is referred to the Gauss Chron (Tedford *et al.*, 1991; Rook, 1993). A similar form is known from the Kuruksai fauna of southern Tajikistan (*Canis* cf. *etruscus* in Sotnikova *et al.*, 1997). The recent morphological study of these canids indicates that a primitive form close in size to the *C. etruscus-arnensis* group occurs in the late Pliocene of Asia. In Europe, *Canis* with similar dimensions appeared in the Costa San Giacomo Faunal Unit of the middle Villafranchian. It is known from the Senéze locality in France, Costa San Giacomo in Italy, and Slivnitsa in Bulgaria (Rook, 1993; Spassov, 1997). Martin (1973) described the Senéze wolf as the new species *C. senezensis.* It is comparable in size with *C. arnensis* being larger on the average than *C. etruscus.* According to dimensions and some dental characters, the canid from the Khapry faunal assemblage is close to *C. senezensis*, and we the attribute it, though with some doubts, to this species.

Family Mustelidae Fischer de Waldheim, 1817

Subfamily Lutrinae Bonaparte, 1838

Genus *Lutra* Brunnich, 1772

*Lutra* sp.

Plate II, fig. 7.

*Lutra* sp.: Baigusheva, 1971, p. 11.

*Material*: incomplete left ramus with alveoli of posterior root of m1 and m2, RSU-1350.

*Locality*: Liventsovka, the Khapry sequence.

*Description and comparison.* There is a fragment of horizontal ramus with the mandibular depth and thickness behind m1, D/T = 12.9/7.0. Massive mandibular proportions, a large root of m2, and its more lingual position in the ramus distinguish this mandible from the specimen RSU-98/2034 that is assigned to *Pannonictis*, and suggest its similarity with Lutrinae. In the Liventsovka otter, the mandibular depth under m1 does not exceed the length of the lower carnassial (m1L = 13.0; D = 11.9). A small mandibular depth differentiates the specimen RSU-1350 from the fossil Aonyxini and implies affinity with Lutrini. Dimensions of the Khapry otter are within the variability range of the genus *Lutra.*

*Discussion.* Lutrinae are very scarce and fragmentary represented in the Pliocene of Europe. Their finds were recorded in the Perrier-Etouaires locality, and separate bones are known from the Saint-Vallier and Kishlang sites. According to Willemsen (1992), the early Pleistocene *Lutra* are unknown in Europe, whereas the specialized *L. simplicidens* Thenius was already widespread there in the middle Pleistocene. The Asian *Lutra* are reported from the late Pliocene of India and China. The origin of recent Eurasian *L. lutra* (L.) is associated with *L. palaeindica* Falc. et Caut. known from the late Pliocene (Upper Siwalik) of India (Pohle, 1919), whereas the Pliocene *L. licenti* Teilhard et Piveteau from the Nihewan, China, has features close to those of *L. canadensis* Schreber (Van Zyll de Jong, 1972) living in Canada. Although records of fossil *Lutra* are relatively scarce, the above rview shows that they were most likely common in the late Pliocene faunas of Eurasia.

Subfamily Galictinae Reig, 1957

Genus *Pannonictis* Kormos, 1931

*Pannonictis nestii* (Martelli, 1906)

Plate I, figs. 8–11.

*Meles* sp.: Baigusheva, 1971, Plate 1, fig. 4.

*Material*: fragmentary anterior left part of a skull; partly broken canine and P4, alveoli of P1, P2, P3, and M1 (RSU-1327); right ramus with p4 and alveoli of p2–m2 (RSU-98/2034).

*Locality*: Liventsovka, the Khapry sequence.

*Description and comparison.* Remains from the Khapry alluvium were directly compared with *Pannonictis pachygnatha* (Teilhard et Piveteau) from Shamar (Mongolia, PIN 3381-197), *P. pliocaenica* Kormos from Etulia, (Moldova, GIN 428-218), *P. nestii* (Martelli) from Valdarno (Italy, type specimen IGF 916, cast AMNH-104715), *Enhydrictis ardea* (Bravard) from Saint-Vallier (France, QSV-150, cast AMNH-26956), and *E. galictoides* Forsyth Major from Sardinia (Italy,

**Plate II.** Carnivores of the Khapry faunal assemblage.

*Pachycrocuta brevirostris*, left ramus, RSU-231: (1) occlusal and (2) lateral views (scale: 2/3 × 1); right lower molar, RSU-231: (3) occlusal view (scale: 1 × 1). *Lynx issiodorensis*, right upper canine, RSU-169: (4) lateral view (scale: 1 × 1). *Acinonyx pardinensis*, right P4, RSU-669: (5) occlusal and (6) lateral views (scale: 1 × 1). *Lutra* sp., fragment of the left ramus without teeth, RSU-1350: (7) lateral view (scale 2 × 1). *Homotherium crenatidens*, fragment of right upper canine, RSU-74: (8) lateral view; left ramus with a canine and p3–m1, RSU-94: (9) lateral view (scale: 1 × 1).

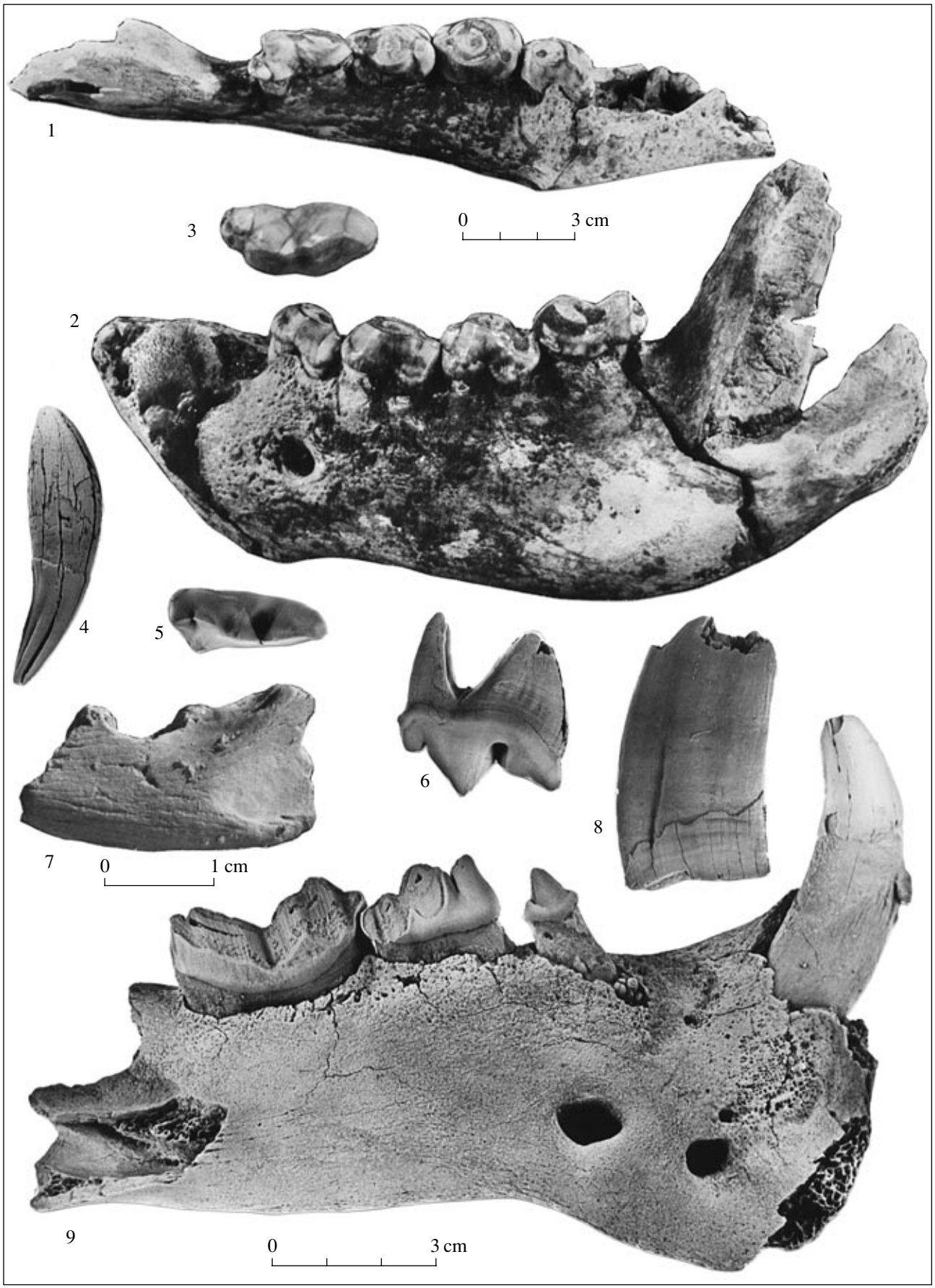
1
3
0
3 cm
2
4
5
6
8
7
0
1 cm
9
0
3 cm

**Table 2.** Measurements of upper teeth of *Pannonictis* and *Enchydrictis*

| Upper teeth | | *Pannonictis nesti* | | *Enchydrictis ardea* |
|---|---|---|---|---|
| | | Liventsovka | Pietrafitta* | Saint-Vallier |
| | | RSU-98 | no. 1749 | OSV-150 |
| I3 | L | 4.5 | – | 4.0 |
| | W | 3.5 al | – | 3.3 al |
| | H | 8.2 al | – | 6.5 al |
| C | L | 7.3 | – | 6.8 |
| | W | 5.8 al | – | 5.1 al |
| L P1 | | 1.0 al | 3.2 | 1.5 al |
| L P2 | | 4.6 al | 4.4 | 4.4 al |
| L P3 | | 6.5 al | 6.6 | 6.4 al |
| L P4 | | 10.8 al | 10.4 | 10.2 al |
| L I3–P4 | | 36.8 | – | 31.9 |
| L C–P4 | | 30.1 | 30.2** | 26.8 |
| L P2–P4 | | 22.0 al | 24.3** | 21.0 al |

*After Rook, 1995;
**After Rook (1995, fig. 2).

**Table 3.** Measurements of mandibles and teeth of *Pannonictis nestii*

| Mandible | Liventsovka | Valdarno Superiore | Pietrafitta* |
|---|---|---|---|
| | RSU-98 | IGF 916, type | no. 1750 |
| L/W p2 | 4.2 al | – | –/2.6 |
| L/W p3 | 6.5 al | 6.4/3.5 | 6.2/3.6 |
| L/W p4 | 7.5 | 6.7/3.5 | 6.8/3.6 |
| L/W m1 | 13.5 al | 12.4/5.0 | 12.5/5.2 |
| L/W m2 | 3.3 al | 3.8/3.9 | 3.2/3.3 |
| L p2–m1 | 30.0 al | 27.0 al | 29.0** |
| L p2–m2 | 34.0 al | 30.4 al | 32.0** |
| L p2–p4 | 17.2 al | 15.0 al | 15.5** |
| L m1–m2 | 17.3 al | 15.8 al | 16.1** |
| DM/WM | 15.1/7.1 | 14.8*/6.3* | 14.5/7.0 |
| LPC | 60.2 | – | 63.2** |

*After Rook, 1995;
**After (Rook, 1995, fig. 3); (DM/WM) the mandible depth/width ratio below m1; (LPC) length from p2 to the posterior margin of a condyle.

type specimen IGF 6089, cast AMNH-89775). For other comparisons we used the data from publications.

Like other Galictinae, the Khapry mustelid had a short muzzle strongly expanded in the area of maxillary zigomatic processes, vertically situated upper canines with a characteristic groove at the anterolateral side of the crown, and a large infraorbital foramen located above the anterior part of P4. Upper incisors are slightly arched. The I3 is large with a high crown and separated from the canine by a diastema, L = 1.5. The upper canine has a strong mesial cingulum, a flattened anterior part of the crown, and a distinct vertical groove. A similar morphology of upper canines is seen in *Enhydrictis ardea* from Saint-Vallier and Tegelen and in the holotype of *P. pliocaenica* (Viret, 1954; Willemsen, 1988; Kormos, 1931). The anterolateral groove occurs on upper canines of *P. pilgrimi* Kormos from Villany, Hungary, and *P. nestii* from Pietrafitta, Italy (L. Rook, 1997, personal communication), as well as in *P. pliocaenica* from Etulia, specimen GIN 428-218.

From the alveoli position in the upper premolar, it is obvious that the single-rooted and reduced P1 is set very close to the mesial side of the canine, and the two-rooted P2 and P3 are disposed in the toothrow without a diastema. P4 has a protocone root positioned slightly anteriorly relative to the paracone, a small hypocone, and well-developed lingual and buccal cingula. Judging from the alveolus morphology, the M1 had a reduced but bifurcated posterobuccal root, and its width was almost equal to the length of P4.

The mandible is relatively low and robust, especially at the base of the ascending ramus. It bears two mental foramina and a masseteric fossa reaching posteriorly the level of the m1 alveolus. Like in other Galictinae mustelids, the angular process in the Liventsovka specimen is short and massive; the lower toothrow is relatively straight with the almost equal length of premolars and molars. The p2 and p3 are two-rooted; p4 lacks accessory cusps and cingulum. According to the alveolus, the lower carnassial was relatively long, and m2 was single-rooted.

The described specimen is distinguishable from *P. pliocaenica* and *P. pachygnatha* owing to its smaller dimensions and a more massive base of the ascending ramus. These features resemble those of *P. nestii* and *P. pilgrimi.* It is also close in size to *E. ardea*, but differs by a maxilla, that is high and thick in the area of posterior root of M1. The Liventsovka form is larger than *E. ardea* (QSV-150) in the maxilla height above P4, the length of I3-P4, and in the height of I3 crown. The mandibular toothrow in the specimen RSU-98/2034 does not correspond in length to that of the skull QSV-150 from the Saint-Vallier. The skull fragment and mandible from the Liventsovka are almost equal in size and morphology to that of *P. nestii* from the Pietrafitta and Valdarno Superiore sites (Tables 2 and 3).

*Discussion.* The Galictinae mustelids are well known from the Pliocene and Pleistocene sediments of Eurasia, where they are represented by two genera *Pannonictis* and *Enchydrictis*, but the taxonomy of fossil Galictinae is still a subject of discussion. Kurtén (1968) and Bjork (1970) consider *Pannonictis* as a synonym of

*Enchydrictis*, though many European researchers interpret them as different genera. The type species *E. galictoides* from the Pleistocene of Sardinia actually represents a highly advanced form, and conceivably, it alone should be included in the genus *Enchydrictis.* However, one more species of galictine mustelids, *E. ardea*, is commonly referred to this genus. The type specimen *"Mustela" ardea* from the Etouaires locality was described on the basis of a mandibular fragment with m1, but nowadays the species is better known owing to the skull QSV-150 from the Saint-Vallier, which was referred to *E. ardea* (Viret, 1954). *E. galictoides* and *E. ardea* are chiefly similar, having a strong postorbital constriction of the skull, whereas in *Pannonictis* this area is wide. The largest species *P. pliocaenica* and *P. pachygnatha* are well distinguishable in both the morphology and measurements, particularly in the mandible index (Sotnikova and Sablin, 1993; Rook, 1995). The taxonomy of relatively small *Pannonictis* forms still remains debatable. In Europe, they are represented by *P. pilgrimi* and *P. nestii*, though some researchers interpret them as synonyms (Ficcarelli and Torre, 1967). These species are placed either in the genus *Pannonictis* and thus considered separately from *E. ardea* (Kormos, 1931; Ficcarelli and Torre, 1967; Rook, 1995), or in the genus *Enchydrictis* as synonyms of *E. ardea* (Viret, 1954; Kurtén, 1968; Willemsen, 1988). In addition, these mustelids are sometimes identified as *Pannonictis ardea* (Rabeder, 1976; Wolsan, 1993). Actually, the dimensions of carnassials in *E. ardea*, (P4L = 10.4, m1L = 11.6), in *P. nestii* (P4L = 10.4, m1L = 11.5–12.6), and in *P. pilgrimi* (P4L = 10.5, m1L = 11.8–13.5) fall within the variation limits of a single species and do not differ from those of the Liventsovka specimen having P4L = 10.8 and m1L = 13.5.[3] Rook believes, however, that *E. ardea* can be distinguished from the galictine mustelids close in size because of a small width of its mandibular ascending ramus in the type specimen from the Etouaires locality and owing to a shortened rostral and flattened frontal area of the skull in specimen QSV-150 from the Saint-Vallier (Rook, 1995). The skull cast QSV-150 studied by one of the authors also implies that *E. ardea* from the Saint-Vallier is most likely a distinct species, but its affinity with *Enchydrictis* or *Pannonictis* genera can be properly discussed based on additional data.

Family Hyaenidae Gray, 1869

Genus *Pliocrocuta* Kretzoi, 1938

*Pliocrocuta perrieri* (Croizet et Jobert, 1828)

Plate I, figs. 12 and 13.

*Hyaena* sp.: Gromov, 1948, p. 45.

*Crocuta* sp.: Baigusheva, 1971, p. 12 (partly).

*Material*: incomplete right ramus with p3 alveolus and p2, GIN-301/10; partly broken left ramus with p3–p4, RSU-1512; left p3, RSU-674; right p2, GIN-300/58.

*Localities*: Liventsovka, RSU-674, RSU-1512; Khapry, GIN-300/58; Morskaya, GIN-301/10; the Khapry sequence.

*Description and comparison.* The Khapry fossils were directly compared with mandibles of *P. perrieri* (Croizet et Jobert) from the Kuruksai locality, Zone MN17 (6 specimens), and with *P. pyrenaica* (Depéret) from the Odessa Catacombs, the uppermost part of Zone MN15 (30 specimens). The size and major morphological characters of the Khapry hyena are within the range of *P. perrieri* features (Table 4). In contrast to *P. pyrenaica*, it has relatively massive premolars with posterior accessory cusplets slightly separated from cingulum. This feature is particularly well observed on p3. All of 23 investigated p3 specimens of *P. pyrenaica* have a posterior accessory cusplet distinctly separated from cingulum.

*Discussion.* Werdelin and Solounias (1991) interpret *P. pyrenaica* as a synonym of *P. perrieri* in contrast to many researchers who consider them as different species (Howell and Petter, 1980; Qiu, 1987). The major argument in support of the former conclusion was a diagram illustrating teeth size variations of *P. perrieri* and *P. pyrenaica*, which are almost identical (Werdelin and Solounias, 1991, fig. 11).

The detailed morphological analysis of *P. pyrenaica* from the Odessa Catacombs and of *P. perrieri* from the Kuruksai and Khapry sites, along with comparison of results with available data on Eurasian *Pliocrocuta*, revealed the following distinctive features of lower teeth of the Ruscinian hyena: the posterior cusplet of premolars is distinctly separated from cingulum; the anterior part of p4 crown is not labially expanded; the metaconid always occurs on dp4; it also occurs on m1 in 22 of 27 specimens; the posterior crest on the protoconid of m1 (protocristid) is generally directed toward the metaconid.

In *P. perrieri*, cingulum on lower premolars is joined to the posterior cusplet; the anterior part of premolar crowns is labially expanded. The metaconid on dp4 is reduced, being missing on m1 in all specimens from the Kuruksai site and in 19 of 22 carnassials of European forms (Kurtén and Crusafont, 1977). The protocristid on m1 is connected (or tends to be connected) with the hypoconid. Based on these data and following the known taxonomy (Howell and Petter, 1980; Qiu, 1987), we interpret *P. perrieri* and *P. pyrenaica* as distinct species.

Genus *Pachycrocuta* Kretzoi, 1938

*Pachycrocuta brevirostris* (Aymard, 1846)

Plate II, figs. 1–3.

*Crocuta* sp.: Baigusheva, 1971, Plate 1, fig. 5.

[3] Measurements are given according to Viret (1954), Schaub (1949), and Rook (1995).

**Table 4.** Measurements of lower teeth of *Pliocrocuta perrieri* and *Pachycrocuta brevirostris*

| Lower teeth | | *Pliocrocuta perrieri* | | | | | | | | *P. brevirostris* | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Khapry | Morskaya | Liventsovka | | Western Europe* | | Kuruksai** | | Liventsovka | | Western Europe* | | collection of GIN*** | |
| | | GIN-300/58 | GIN-301/10 | RSU-1512 | RSU-674 | n | m–m | n | m–m | RSU-231 | | n | m–m | n | m–m |
| | | | | | | | | | | right | left | | | | |
| p2 | L | – | 16.0 | – | – | 14 | 14.0–17.7 | 3 | 12.4–16.4 | 19.1 | 19.2 | 4 | 18.0–19.0 | 4 | 18.6–19.4 |
| | W | – | 9.9 | – | – | 13 | 9.3–12.2 | 2 | 9.8–10.5 | 13.0 | 13.4 | 4 | 12.3–14.5 | 4 | 13.2–14.5 |
| p3 | L | 20.4 | – | 21.2 | – | 16 | 19.5–22.9 | 6 | 19.5–21.5 | 23.0 | 23.6 | 6 | 22.5–26.0 | 5 | 22.4–25.9 |
| | W | 14.3 | – | 15.0 | – | 13 | 13.3–16.6 | 4 | 13.3–16.6 | 16.8 | 17.2 | 4 | 15.6–19.0 | 4 | 17.3–18.9 |
| p4 | L | – | – | 22.8 | 23.9 | 19 | 21.4–25.5 | 7 | 20.4–23.9 | 25.3 | 25.0 | 7 | 25.5–28.1 | 5 | 25.7–26.7 |
| | W | – | – | 15.0 | 13.4 | 16 | 11.8–16.1 | 4 | 13.9–14.5 | 16.7 | 16.1 | 6 | 16.2–17.8 | 5 | 15.5–18.9 |
| m1 | L | – | – | – | – | 22 | 23.4–26.9 | 6 | 23.7–26.3 | 27.8 | 28.2 | 4 | 27.5–31.2 | 4 | 27.7–30.0 |
| | W | – | – | – | – | 18 | 10.8–14.6 | 4 | 12.9–13.2 | 15.1 | 14.8 | 4 | 13.2–15.0 | 3 | 14.9–15.4 |
| | Lt | | | | | 19 | 19.4–22.8 | 6 | 19.8–21.9 | 24.5 | – | 4 | 23.0–25.8 | 3 | 23.9–25.3 |

*After Howell and Petter (1980); **after Sotnikova (1989); ***Early Pleistocene remains from the Nalaikha (Mongolia), Lakhuti (Tajikistan), Zasukhino (Russia, Transbaikal region) Taman', and Volga sites (Russia, European part); collection of GIN; (m–m) minimum and maximum values.

*Material*: mandible with well-preserved condyle and angular processes on the right ramus, canines and incisors are missing; RSU-231.

*Locality*: Liventsovka, the Khapry sequence.

*Description and comparison.* The collection includes a mandible of a large hyena. The mandible lengths L = 244.5 and L = 232.0 are measured from the alveolus of i1 to the angular process and to the condyle, respectively. The morphological characters are typical of *Pachycrocuta brevirostris* in every respect. The mandible is very massive and high in the horizontal ramus. Its depth is D = 55.0 before p2, D = 60.0 below m1, and D = 48.0 between p3 and p4. The mandible thickness beneath p3 is T = 29.1. These measurements agree well with those of the three mandibles of *P. brevirostris* from the lower Pleistocene of Macedonia (Kurtén and Garevski, 1989, tab. 3, p. 146).

The lower incisors and canines are notably large: i1, Lal = 8.3; i2, Lal = 10.9; i3, Lal = 15.2; c1, Lal = 28.5. The p2 bears a small anterior accessory cusp and a larger posterior one. Its dimensions exceed the variability range known for *P. perrieri* and correspond to that of *P. brevirostris* (Table 4). The worn p3 is more robust than p4. It has a small anterior accessory cusp, a large posterior one, and a well-developed anterolabial cingulum. The occurrence of anterior accessory cusps on p2 and p3 is rarely seen in *P. brevirostris* samples. They are missing in five *P. brevirostris* specimens from the Asian localities of the former USSR (early–middle Pleistocene, GIN collection) and in European forms (Kurtén and Garevski, 1989). However, they occur in *P. brevirostris* from the late Villafranchian locality Apollonia 1 (Koufos and Kostopoulos, 1997). The p4 is longer and narrower than p3, its anterior and posterior accessory cusps are high and slightly separated from the main cusp. The carnassial is long relative to p4, the metaconid is absent, and the two-cusped talonid is inconsiderably reduced.

The Liventsovka *Pachycrocuta* differs from the type species *P. brevirostris* from the Sainzelles site by lesser dimensions, by anterior accessory cusp present on p2, and by more reduced p4. *P. brevirostris licenti* (Pei) from the Pliocene of China has the three-cusped talonid (Qiu, 1987) and short p4 (Koufos, 1992, fig. 11). The latter character discriminates it from all European forms and suggests similarity with the *Pachycrocuta* form of the Liventsovka site. However, the latter looks more advanced as having the two-cusped talonid.

*Discussion.* The Eurasian large crocutoid hyena was repeatedly discussed by different researchers. It was considered within the limits of the *Hyaena* (Kurtén, 1956; Kurtén and Garevski, 1989) and *Pachycrocuta* (Ficcarelli and Torre, 1970) genera. Qiu (1987) placed it into the *Pliohyaena*, but Werdelin and Solounias (1991) returned it, however, in the genus *Pachycrocuta* in the old nomenclature. The following diagnosis was given for *P. brevirostris*: large size, massive teeth, wide premolars, an anterior accessory cusp well developed only on p4, m1 considerably longer than p4 and bearing a reduced two-cusped talonid but lacking metaconid (Howell and Petter, 1980).

The present-day studies show that some diagnostic features of *P. brevirostris*, such as occurrence of anterior cusps of p2 and p3, and the number of talonid cusplets, can vary. Kurtén and Garevski (1989) marked

**Table 5.** Measurements of upper P4 in different Villafranchian *Acinonyx* and *Megantereon* taxa

| P4 | *Acinonyx pardinensis* | | | | *Acinonyx aicha* | | | | *Megantereon cultridens* | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Liventsovka | Western Europe, Bonifay, 1971; Kurtén and Crusafont, 1977 | | | Northern Africa, Geraads, 1997 | | | | Western Europe, Turner, 1987 | |
| | RSU-669 | n | m–m | Md | n | m–m | Md | n | m–m | Md |
| L | 30.1 | 9 | 23.3–28.2 | 26.4 | 4 | 28.3–32.1 | 30.2 | 7 | 29.5–35.5 | 31.7 |
| W | 12.6 | 4 | 11.0–14.1 | 12.4 | 4 | 9.2–14.3 | 12.3 | 7 | 11.8–14.6 | 13.6 |
| W pc/mt | 10.2 | 9 | 9.0–11.0 | 9.5 | 3 | 9.5–12.3 | 10.5 | 7 | 9.4–11.2 | 10.1 |
| L pc | 12.6 | 9 | 9.0–11.2 | 10.5 | 2* | 12.1–12.6 | 12.3 | 7 | 10.9–12.5 | 11.5 |
| L ms | 12.3 | 9 | 9.5–12.1 | 10.8 | 2* | 11.9–12.5 | 12.2 | 7 | 11.5–13.4 | 12.3 |

*After Geraads (1997, fig. 8); (Wpc/mt) width at the paracone and metastyle juncture; (Lpc) paracone length; (Lms) metastyle length; (m–m) minimum and maximum values.

that in many cases the talonid of m1 of *P. brevirostris* has a single cutting cusplet, and that it is most typical of this hyena, though two or three talonid cusplets can also occur however. They do not associate the number of talonid cusplets of m1 in *Pachycrocuta* with the geologic age. However, our data indicate that m1 with a single talonid cusplet prevails in *P. brevirostris* of the Galerian faunas (terminal early–middle Pleistocene), whereas the two-cusped talonids are more common in the late Villafranchian forms. The increase of premolar robustness, absence of anterior accessory cusps in p2 and p3, the talonid reduction and decrease in number of its cusplets, and the lack of metaconid on m1, should be most likely considered as advanced characters in the *Pachycrocuta* evolution.

*P. brevirostris* from the Khapry assemblage is similar to the late Villafranchian European forms because of occurrence of anterior cusps of p2 and p3, and owing to presence of a moderately reduced talonid with two cusplets on m1. The relatively small dimensions of p4 suggest its similarity with the late Pliocene *P. brevirostris licenti* from China.

Family Felidae Gray, 1821

Genus *Lynx* Kerr, 1792

*Lynx issiodorensis* (Croizet et Jobert, 1828)

Plate II, fig. 4.

*Lynx* sp.: Baigusheva, 1971, p. 12, Plate 1, fig. 7.

*Material*: right upper canine, RSU-169.

*Locality*: Liventsovka, the Khapry sequence.

*Description and comparison.* The large upper canine has a double groove at the anterolabial side of the crown typical of *Lynx*. Its length L = 11.5 slightly exceeds the variability range L = 8.5–10.5 inferred by Kurtén and Crusafont (1977) for 13 specimens of *Lynx issiodorensis* from different European Villafranchian localities, whereas the width W = 8.4 is within the corresponding limits W = 6.5–8.4.

Genus *Acinonyx* Brookes, 1828

*Acinonyx pardinensis* (Croizet et Jobert, 1828)

Plate II, figs. 5 and 6.

*Material*: right P4, RSU-669; a distal fragment of the left humerus; the deltoid tuberosity area and medial epicondyle are broken, RSU-97.

*Localities*: Morskaya (RSU-669), Liventsovka (RSU-97), the Khapry sequence.

*Description and comparison.* The size of P4 is within its range of variation in large late Villafranchian felids, such as *Megantereon cultridens* (Cuvier) and *Panthera gombaszoegensis* (Kretzoi). It differs from that of *Panthera* by a more reduced and posteriorly placed protocone. Like in *Megantereon* forms, the protocone of specimen RSU-669 is reduced but differs from P4 of *Megantereon* in a poorly developed parastyle and more straight labial line of the tooth crown. The poorly developed protocone situated far behind the parastyle and united anterior roots of the Khapry carnassial are similar to these characters of *Acinonyx*. The measurements of this tooth slightly exceed the range of length variation of P4 in the European Pliocene *Acinonyx pardinensis*, but they are within that of *A. aicha* Geraads from the upper Pliocene of North Africa (Table 5).

The humerus RSU-97 is lesser in size than that of *Homotherium, Megantereon*, and *Panthera gombaszoegensis*, being close to that of the leopard and extinct cheetah. It differs from this bone of *Panthera pardus* L. because of a shaft more compressed mediolaterally and of epicondylar foramen situated more vertically. In the relatively slender proportions, the Liventsovka form resembles cheetahs, and its size is close to that of *Acinonyx pardinensis, Miracinonyx inexpectatus* (Cope), and *M. trumani* (Orr) (Van Valkenburg *et al.*, 1990, tab. 3, p. 440). The estimated humerus parameters of the Liventsovka form are: the approximate length L = 240.0–250.0, minimum mediolateral shaft diameter S = 19.0, and distal articular width W = 42.3, against corre-

**Table 6.** Measurements of the *Homotherium* lower teeth

| Localities | p3 | | p4 | | m1 | |
|---|---|---|---|---|---|---|
| | L | W | L | W | L | W |
| Valdarno Superiore (Ficcarelli, 1979) | 7.9 | 4.5 | 20.4 | 9.2 | 31.5 | 12.7 |
| | 9.5 | 5.5 | – | – | 31 | 13.1 |
| | 12.0 | 6.4 | 23.5 | 10.4 | 33.5 | 13.4 |
| | – | – | 22.5 | 10.4 | 30 | 13.4 |
| | – | – | 24.7 | 10 | 33.9 | 13.5 |
| Senéze (Ballesio, 1963) | 8.0 | – | 22 | – | 32 | – |
| Rocca Neyra (Bonis, 1976) | 6.5 | – | 18.2 | – | 32.5 | – |
| Liventsovka, collection of RRM, RSU-94 | 10.0 | – | 24.7 | – | 35.4 | – |
| Gräunceanu (Bolomey, 1965) | 6.7 | – | 20.5 | – | 32 | – |
| Kuruksai, collection of PIN 3120 | 8.0 | – | 21.5 | – | 29.9 | – |
| Odessa Catacombs, collection of OSU-3197, 3236; collection of KPM-1007 | – | – | 23.2 | – | 30 | – |
| | 12.7 | 7.1 | 22.2 | 9.6 | 27.5 | 13 |
| | 13.3 | 7.7 | 23.7 | 10.3 | 28.3 | 12.2 |
| | – | – | 23.1 | 10.2 | 29.2 | 12.2 |
| | 12.8 | 7.4 | 22.7 | 10.5 | 28.3 | 12.5 |
| Kvabebi (Vekua, 1972) | 9.0 | – | 20 | – | 26 | – |
| | – | – | 21 | – | 25 | – |
| Udunga, collection of GIN | – | – | 18.5 | 8.5 | 25.8 | 11 |

sponding characters of fossil cheetahs L = 269.0–273.0, S = 18.1–21.5, and W = 35.6–42.8.

*Discussion.* The new cheetah species *A. aicha* Geraads was recently described from the upper Pliocene Ahl al Oughlam locality, Casablanca, Morocco (Geraads, 1997). Its upper carnassial is slightly larger than in the Pliocene *A. pardinensis* of Europe and corresponds in size to the specimen from the Morskaya locality. In distinction from the European form, the African cheetah has a more complicated morphology of P3 with an anterior accessory cusp, but unfortunately we lack the material for a thorough comparison of this feature. The upper carnassial proportions and morphology of the Khapry cheetah are identical to those of *A. pardinensis*, and larger dimensions do not imply necessity of taxonomic discrimination between African and European species.

Genus *Homotherium* Fabrini, 1890

*Homotherium crenatidens* (Fabrini, 1890)

Plate II, figs. 8 and 9.

*Machairodus* sp.: Gromov, 1948, p. 45; Baigusheva, 1971, Plate 1, fig. 6.

*Material*: fragment of a right upper canine, RSU-74; right ramus with c1 and p3-m1, incisors and ascending ramus are missing, RSU-94.

*Locality*: Liventsovka, the Khapry sequence.

*Description and comparison.* Species described below was directly compared with the *Homotherium* forms from the Odessa Catacombs, Kvabebi, Kuruksai and Udunga localities; data on other homotheres are from publications.

The flattened upper canine is serrated; its anteroposterior transverse diameters are 27.0 and 12.5, respectively. The mandible belongs to a large *Homotherium*, dimensions of which are within the variability of *Homotherium crenatidens.* Length L = 129.0 of the lower toothrow c1–m1 is close to that (L = 132.0) of the largest *H. nestianum* Fabrini described from the Rocca Neyra locality (Bonis, 1976). Like other homotheres, the Liventsovka form has all teeth serrated and premolars reduced. The symphysis is deep, the mental flange and crest are well developed. Incisors and canine are elevated relative to other teeth. Two large of three mental foramina are located below the c1–p3 diastema and p3, respectively. The third small foramen is set above the first one. All three foramina are connected inside the mandible. The diastema length value is Lc1–p3 = 37.0. The canine located closely to incisors has two sharpened serrated ridges, the posterior one in a central position and the anterior ridge situated at the anterolingual side of the crown. The p3 is separated from p4 by a diastema, L = 2.5; the anterior and posterior crests of the main cusp on p3 are serrated. The anterior accessory cusplet on p3 is formed by cingulum, the posterior one is more distinct and well-separated from the main cusp. The cingulum is well traceable posteriorly at the

labial side of the crown, whereas at the lingual side it is missing. The p3 is single-rooted, unworn; it was most likely nonoperating. Its crown is distinctly inclined posteriorly. All four cusplets of p4 are also posteriorly inclined. The first one is well separated from the others; the fourth small cusplet grades into cingulum at the posterolingual side of the tooth. The remaining cusplets are worn. The exposed roots are united for the one third of their length. The posterior part of p4 crown is overlapped in a toothrow with the paraconid of m1. The carnassial is very large, lacking traces of talonid and metaconid.

*Discussion.* As indicated by Ficcarelli (1979), distinctions between *H. nestianum* and *H. crenatidens* from the Valdarno Superiore are within the individual variability of a single *Homotherium* species. The studied series of *Homotherium* skulls from the Crespiá locality showed that the observed variability resulted from a sexual dimorphism, and this permitted the interpretation of all Pliocene and Pleistocene European *Homotherium* species as synonyms of *H. crenatidens* (Pons-Moyá and Moyá-Solá, 1992).

Asian forms are closely similar to European ones, and nowadays the numerous *Homotherium* remains from the middle Villafranchian Kuruksai locality, Tajikistan, are also assigned to *H. crenatidens* (Sotnikova, 1989). In Europe, the most informative finds of Pliocene homotheres are known from the middle Villafranchian; the early Villafranchian West European forms have not been used in the comparative analysis because of the data paucity. The older *Homotherium* forms are better represented in the East European faunas from the Odessa Catacombs (Ukraine, terminal part of Zone MN15) and from Zone MN16 of the Kvabebi section of Georgia (Alekseev, 1945; Vekua, 1972). Distinctive features of homotheres from these localities are lesser average dimensions, slightly reduced p3, and m1 a little longer than p4 (Table 6). The same features are characteristic of *Homotherium* remains from the Udunga site, Transbaikal region, Zone MN16a (Sotnikova and Kalmykov, 1991).

The Eurasian material demonstrates that dimensions of skull, upper canine, and diastema c1–p3 are strongly variable in homotheres. Also variable are the development degree of p3 and its position in a mandible either with, or without diastema between p3 and p4. In most cases, these variations presumably imply sexual dimorphism, though the evolutionary changes were important as well. The tendency of premolars to be simplified and reduced characterizes changes during the lifetime of homotheres. Turning to be out of functioning, p3 significantly varies in size and position in a mandible. In contrast, p4 became gradually shorter relative to m1. This character enables distinction between the Ruscinian–early Villafranchian and younger homotheres. Based on this feature, we place the Khapry *Homotherium* into the second group (Fig. 4).

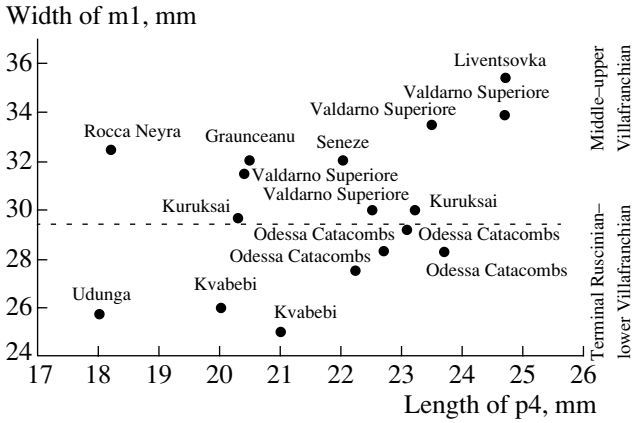


**Fig. 4.** Length of lower p4 versus m1 of some *Homotherium* species.

## CONCLUSION

Carnivores of the Khapry fauna are represented forms typical of the European Villafranchian, and many of them were concurrently distributed in Asia as well.

The stratigraphic range of *Pliocrocuta perrieri, Homotherium crenatidens, Acinonyx pardinensis*, and *Lynx issiodorensis* covers the whole Villafranchian, whereas the appearance and extinction of *Nyctereutes megamastoides, Pachycrocuta brevirostris*, and *Canis* s. str. are recorded at different levels of the interval.

Based on changes in composition of large mammal assemblages, a number of faunal units and events marking their boundaries were distinguished in the West European Villafranchian. The carnivores were found to be good biostratigraphic markers, particularly in the middle-upper Villafranchian interval by transition from the Costa San Giacomo to the Olivola Faunal Unit (Azzaroli *et al.*, 1988; Torre *et al.*, 1992; Rook and Torre, 1996). This interval is marked by disappearance of *Nyctereutes megamastoides* that did not transit into the late Villafranchian. The appearance of genus *Pachycrocuta* at the beginning of the late Villafranchian is known as the "*Pachycrocuta brevirostris* faunal event." *Canis* s. str. first appeared in the Costa San Giacomo Faunal Unit, whereas wolf- and coyote-like *Canis etruscus* and *C. arnensis* became widespread later on, in the Olivola Faunal Unit, ("wolf–event" sensu Azzarolli, 1983).

The Khapry carnivore assemblage appears to be not ordinary because of the joint occurrence of *Nyctereutes* and *Pachycrocuta*, the asynchronous taxa according to the West European scale. On the other hand, this fauna includes *Pannonictis nestii* known from the late Villafranchian of Europe and medium-sized *Canis* forms, the wide dispersal of which began since the Olivola Faunal Unit.

The dynamics of carnivore development across the Pliocene–Pleistocene boundary was thoroughly studied in Western Europe. The faunal changes that took place

in the East European mammal assemblages and Carnivora evolution in the eastern regions are imperfectly understood so far, and hence the Khapry assemblage needs in special comments, particularly with respect to index genera *Nyctereutes, Canis*, and *Pachycrocuta.*

The genus *Nyctereutes* unknown in the Pleistocene is one of most common members of the Pliocene mammal assemblages from Europe. The latest *N. megamastoides* forms are recorded in the Senéze locality of Europe (Turner, 1992). The age range of fauna from this site is considered to be within the late middle Villafranchian, correlative with the pre-Olduvai part of the Matuyama Chron (Rook and Torre, 1996). In Asia, finds of *N. megamastoides* are known from the Kvabebi site of Georgia (early Villafranchian) and from the middle Villafranchian Zil'fi, Tutak, and Kuruksai localities of Tajikistan. Similar forms are recorded in the Pliocene of the Transbaikal region (Russia) and China (Vekua, 1972; Sotnikova *et al.*, 1997; Tedford and Qiu, 1991). The latest *N. megamastoides* was described in the Caspian region of Asia as a component of the Palan-Tyukan fauna close in age to the Senéze assemblage (Sotnikova and Sablin, 1993). Consequently, stratigraphic range of this species in Asia is limited, like in Europe, by the middle Villafranchian, and presence of *Nyctereutes* remains in the Khapry fauna of the Azov region thus indicates the pre-Olduvai age of the latter.

The genus *Canis* migrated to Europe from Asia. As noted above, the earliest members of the genus are known from the Mazegou Formation of China, where it is correlated with the Gauss Chron, and from the early middle Villafranchian of Tajikistan (Tedford *et al.*, 1991; Rook, 1993; Sotnikova *et al.*, 1997). *Canis* cf. *senezensis* from the Khapry sequence can be considered as the earliest representative indicative of the "*Canis*-event" in Eastern Europe. Accordingly, presence of *Canis* forms in the Khapry fauna do not contradict its reference to the middle Villafranchian.

*Pachycrocuta brevirostris* is a common component of the early and middle Pleistocene faunal assemblages of Eurasia. In Europe, it is first recorded in the Olivola Faunal Unit, being known from many localities from England to Greece. Its appearance marks the beginning of the late Villafranchian and represents one of major events in the biochronologic history of West European mammals (Torre *et al.*, 1992). In Asia, *P. brevirostris* was found in Russia (Transbaikal region), Kazakhstan, Tajikistan, Mongolia, and China. Its earliest occurrence is recorded in South African sediments (Makapansgat site) of 3.0 Ma old, and this hyena is also known from Asian localities presumably close in age to the African site (Turner and Anton, 1996). The peculiar subspecies *P. brevirostris licenti* was detected in the Nihewan fauna of China (Teilhard de Chardin and Piveteau, 1930; Qiu, 1987), stratigraphic position of which is nowadays defined within the pre-Olduvai part of the Matuyama Chron (Tedford *et al.*, 1991). According to certain characters, the *Pachycrocuta* species from the Nihewan site is similar to the Liventsovka hyena. Thus, *P. brevirostris* from the Khapry faunal assemblage conceivably indicates that the genus *Pachycrocuta* could appear in Eastern Europe earlier than in the western regions.

*Pannonictis nestii* is widespread in the late Villafranchian of Europe. The galictoid mustelid *"Martes" crassa* described from the Pliocene deposits of the Yushe Depression, northern China (Teilhard de Chardin and Leroy, 1945), is either conspecific, or represents a geographical variety of *P. nestii.* The appearance of mustelid close to *P. nestii* in the Pliocene of China also indicates the Asian center of this form expansion to Europe.

In general, the Asian influence on the fauna of the Azov region was reasonably strong, as we believe. Apart from certain Carnivora forms, which appeared here earlier than in Western Europe by the invasion from the east, the Khapry faunal assemblage contains typical Asian elements, the westward penetration which was either limited, or did not take place. Among these are representatives of *Palaeotragus, Elasmotherium, Paracamelus* (two species), and *Struthio* genera.

The morphological study of the Khapry Carnivora revealed that *Homotherium* remains are closer to forms from the middle and late Villafranchian of Eurasia. According to the degree of evolution of the mandibular angular process, *Nyctereutes megamastoides* corresponds to *N. megamastoides* from the Saint-Vallier site of France (middle Villafranchian). The Khapry *Canis* shows characters more primitive than those of *C. etruscus* and *C. arnensis* from the late Villafranchian of Europe.

Thus, the Carnivora forms suggest the middle Villafranchian age of the Khapry faunal assemblage (the Saint-Vallier to Costa San Giacomo faunal units).

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## REFERENCES


Alekseev, A.K., *Epimachairodus* from the Pliocene of Odessa, *Dop. AN URSR*, 1945, no. 314, pp. 10–14.

Alekseeva, L.I., *Teriofauna rannego antropogena Vostochnoi Evropy* (Terrestrial Fauna of the Early Anthropogene of Eastern Europe), Moscow: Nauka, 1977, issue 300.

Azzaroli, A., Quaternary Mammals and the "End-Villafranchian" Dispersal Event. A Turning Point in the History of Eurasia, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 1983, vol. 44, pp. 117–139.

Azzaroli, A., De Giuli, C., Ficsarelli, G., and Torre, D., Late Pliocene to Early Mid-Pleistocene Mammals in Eurasia: Faunal Succession and Dispersal Events, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 1988, vol. 66, pp. 77–100.

Baigusheva, V.S., Fossil Terrestrial Fauna of the Liventsovka Quarry (the Northeastern Azov Region), *Materialy po faunam antropogena SSSR* (Materials on Anthropogene Faunas of the USSR), Moscow: Nauka, 1971, vol. 49, pp. 5–28.

Baigusheva, V.S., To the Skull Morphology of Large Deer of the Khapry Assemblage, *Paleoteriologiya* (Paleoteriology), Moscow: Nauka, 1994, pp. 236–252.

Ballesio, R., Monographie d'un *Machairodus* du gisement villafranchien de Senéze: *Homotherium crenatidens* Fabrini, *Trav. Lab. Geol. Lyon, N.S*, 1963, no. 9.

Bjork, P.R., The Carnivora of the Hagerman Local Fauna (Late Pliocene) of Southwestern Idaho, *Trans. Amer. Phil. Soc., N.S*, 1970, vol. 60, no. 7, pp. 3–54.

Bolomey, A., Die Fauna zweier villafrankischer Funstellen in Rumanien, *Ber. Geol. Ges. DDR*, 1965, vol. 10, no. 1, pp. 77–88.

Bonifay, M.F., Carnivores quaternaires du Sud–Est de la France, *Mém. Mus. Nat. Hist., Nat. Sér. C*, 1971, vol. 21, no. 2, pp. 43–377.

Bonis, L., Un Félidé a longues canines de la colline de Perrier (Puy-De-Dôme), *Ann. Paléontol*, 1976, vol. 62, pp. 9–196.

Czyżewska, T., *Nyctereutes sinensis* Schlosser (Canidae, Mammalia) from the Pliocene Breccia in Wże (Poland), *Acta Zool. Cracoviensia*, 1969, no.14, pp. 442–450.

Ficcarelli, G., The Villafranchian Machairodonts of Tuscany, *Palaeontogr. Ital.*, 1979, vol. 71, pp. 17–26.

Ficcarelli, G. and Torre, D., Il mustelide *Enchydrictis galictoides* del Pliocene della Sardegna, *Palaeontogr. Ital.*, 1967, vol. 33, pp. 139–160.

Ficcarelli, G. and Torre, D., Remarks on the Taxonomy of Hyaenids, *Palaeontogr. Ital.*, 1970, vol. 66, pp. 13–33.

Geraads, D., Carnivores du Pliocenè terminal de Ahl al Oughlam (Casablanca, Maroc), *Geobios*, 1997, vol. 30, no. 1, pp. 127–164.

Gromov, V.I., Paleontological and Archaeological Substantiation of Quarternary Continental Stratigraphy of the USSR, *Tr. Inst. Geol. Nauk, Ser. Geol.,* Vyp. 64, 1948, no. 17, pp. 1–520.

Howell, F.C. and Petter, G., The *Pachycrocuta* and *Hyaena* Lineages (Plio-Pleistocene and Extant Species of the Hyaenidae), *Geobios*, 1980, vol. 13, no. 4, pp. 579–623.

Kormos, T., *Pannonictis pliocaenica* n. g., n. sp., a New Giant Mustelid from the Late Pliocene of Hungary, *Ann. Inst. Reg. Hung. Geol.*, 1931, vol. 29, no. 3, pp. 167–177.

Koufos, G.D., The Pleistocene Carnivores of the Mygdonia Basin (Macedonia, Greece), *Ann. Paleontol. (Vert.-Invert.)*, 1992, vol. 78, no. 4, pp. 205–257.

Koufos, G.D. and Kostopoulos, D.S., New Carnivore Material from the Plio-Pleistocene of Macedonia (Greece) with the Description of a New Canid, *Münchner Geowiss. Abh. A*, 1997, vol. 34, pp. 33–63.

Kurtén, B., The Status and Affinities of *Hyaena sinensis* Owen and *Hyaena ultima* Matsumoto, *Amer. Mus. Nov.*, 1956, no. 1764, pp. 1–48.

Kurtén, B., *Pleistocene Mammals of Europe*, London: Weidenfeld and Nicolson, 1968.

Kurtén, B. and Crusafont, P.M., Villafranchian Carnivores (Mammalia) from la Puebla de Valverde (Teruel, Spain), *Comment. Biol. Soc. Sci. Fennica*, 1977, vol. 85, pp. 1–39.

Kurtén, B. and Garevski, R., Giant Hyena, *Hyaena brevirostris* Aymard (Mammalia, Carnivora), from the Middle Pleistocene of Manastirec, Yugoslavia, *Ann. Zool. Fennici*, 1989, vol. 26, pp. 145–147.

Martin, R., Les Affinites de *Nyctereutes megamastoides* (Pomel) canide du gisement villafranchien de St. Vallier (Drôme, France), *Palaeovertebrata*, 1971, vol. 4, no. 2, pp. 39–66.

Martin, R., Trois nouvelles especes de Caninae (Canidae, Carnivora) des gisements Plio-Villafranchiens d'Europe, *Doc. Lab. Geol. Fac. Sci. Lyon*, 1973, vol. 57, pp. 87–96.

Pohle, H., Die Unterfamilie der Lutrinae, *Arciv Naturgeschicte*, 1919, Ser. A, vol. 85, no. 9.

Ponds Moyà, J. and Moyà Solà, S., Observacions sobre l'evolucio i biologia del genere Homotherium Fabrini, 1890, (Mammalia, Carnivora), *Boll. Soc. Hist. Nat. Balears,* 1992, vol. 35, pp. 87–92.

Qiu, Z.-X., Die Hayeniden aus dem Ruscinicum und Villafranchium Chinas, *Münchner Geowiss. Abh. A*, 1987, vol. 9.

Rabeder, H., Die Carnivora (Mammalia) aus dem Altpleistozan von Deutsch-Altenburg 2, *Beitrag. Palaont. Osterr.*, 1976, no. 1.

Rook, L., I Cani dell'Eurasia dal Miocene superiore al Pleistocene medio, *Doctoral Dissertation*, Florence: Florence Univ., 1993.

Rook, L., *Pannonictis nestii* (Carnivora, Mammalia) from the Late Villafranchian of Pietrafitta (Umbria, Italy), *Eclog. Geol. Helv.*, 1995, vol. 88, no. 3, pp. 853–864.

Rook, L. and Torre, D., The Wolf-Event in Western Europe and the Beginning of the Late Villafranchian, *N. Jb. Geol. Paläont. Mh.*, 1996, vol. 8 pp. 495–501.

Sardella, R., Abbazzi, L., Argenti, P., *et al.*, Mammal Faunal Turnover in Italy from the Middle Pliocene to the Holocene, *Proc. of the SEQS-Euro Mam. Symposium: The Dawn of the Quaternary*, 1998, pp. 499–511.

Schaub, S., Revision de quelcues carnassiers villafranchien du niveau des Etouaires, *Eclog. Geol. Helv.*, 1949, vol. 42, pp. 492–506.

Sharapov, Sh., New Find of *Nyctereutes* Temminck 1819 in Tajikistan, *Dokl. Akad. Nauk TadzhSSR*, 1981, vol. 24, no. 3, pp. 190–194.

Soria, D. and Aguirre, E., El Canido de Laina: revision de los *Nyctereutes* fossiles, *Trab. Sobre Neogene-Quaternario, Madrid*, 1976, no. 5, pp. 83–115.

Sotnikova, M.V. and Kalmykov, N.P., Pliocene Association of Carnivores in the Udunga Locality (Western Transbaikal Region), *Paleogeografiya i biostratigrafiya pliotsena i antropogena* (Pliocene to Anthropogene Paleogeography

and Biostratigraphy), Moscow: Geol. Inst. RAN, 1991, pp. 146–159.

Sotnikova, M.V. and Sablin, M.V., The Late Villafranchian Association of Carnivores from the Palan-Tyukan Locality (Eastern Transcaucasia, Azerbaijan Republic), *Materialy po mezozoiskoi i kainozoiskoi istorii nazemnykh pozvonochnykh* (Data on Mesozoic and Cenozoic History of Terrestrial Vertebrates), Moscow: Nauka, 1993, vol. 249, pp. 134–145.

Sotnikova, M.V., Dodonov, A.E., and Pen'kov, A.V., Upper Cenozoic Bio-Magnetic Stratigraphy of Central Asian Mammalian Localities, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 1997, vol. 133, pp. 243–258.

Sotnikova, M.V., *Khishchnye mlekopitayushchie pliotsena–rannego pleistotsena (stratigraficheskoe znachenie)* (Carnivorous Mammals of the Pliocene–Early Pleistocene: Stratigraphic Implications), Moscow: Nauka, 1989.

Spassov, N., Villafranchian Succession of Mammalian Megafaunas from Bulgaria and the Biozonation of South-East Europe, *Actes du Congrés Biochrom'97, Mem. Trav. E.P.H.E., Inst. Montpellier*, 1997, vol. 21, pp. 669–676.

Tedford, R.H. and Qiu, Z.-X., Pliocene *Nyctereutes* (Carnivora: Canidae) from Yushe, Shanxi, with Comments on Chinese Fossil Racoon-Dogs, *Vertebr. Palasiatica*, 1991, vol. 29, pp. 176–189.

Tedford, R.H., Flynn, L.J., Qiu, Z.-X., *et al.*, Yushe Basin, China: Palaeomagnetically Calibrated Mammalian Biostratigraphic Standart for the Late Neogene of Eastern Asia, *J. Vertebr. Palaeontol.*, 1991, vol. 11, no. 4, pp. 519–526.

Tedford, R.H., Taylor, B.E., and Wang, X., Phylogeny of the Caninae (Carnivora: Canidae): the Living Taxa, *Amer. Mus. Nov.*, 1995, no. 3146, pp. 1–37.

Teilhard de Chardin, P. and Leroy, P., Les Mustélidés de Chine, *Inst. Géobiol. Peking*, 1945, no. 12.

Teilhard de Chardin, P. and Piveteau, J., Les Mammiferes fossiles de Nihowan (Chine), *Ann. Paleontol.*, 1930, vol. 19, pp. 10–128.

Tesakov, A.S., Evolution of Small Mammal Communities from the South of Eastern Europe near the Plio-Pleistocene Boundary, *Acta Zool. Cracov.*, 1995, vol. 38, no. 1, pp. 121–127.

Torre, D., Albianelli, A., Azzaroli, A., *et al.*, Palaeomagnetic Calibration of Late Villafranchian Mammalian Faunas from the Upper Valdarno, Central Italy, *Mem. Soc. Geol. Ital.,* 1993, vol. 49, pp. 335–344.

Torre, D., Ficcarelli, G., Masini, F., Rook, L., and Sala, B., Mammal Dispersal Events in the Early Pleistocene of Western Europe, *Courier Forsch.-Inst. Senckenberg*, 1992, no. 153, pp. 51–58.

Turner, A., *Megantereon cultridens* from Plio-Pleistocene Age Deposits in Africa and Eurasia, with Comments on Dispersion and the Possibility of a New Word Origin (Mammalia, Felidae, Machairodontinae), *J. Palaeont*, 1987, vol. 61, pp. 1256–1268.

Turner, A., Villafranchian-Calerian Larger Carnivores of Europe: Dispersions and Extinctions, *Courier. Forsch.-Inst. Senckenberg*, 1992, vol. 153, pp. 153–160.

Turner, A. and Antón, M., The Giant Hyaena, *Pachycrocuta brevirostris* (Mammalia, Carnivora, Hyaenidae), *Geobios*, 1996, vol. 29, no. 4, pp. 455–468.

Van Valkenburgh, B., Grady, F., and Kurtén, B., The Plio-Pleistocene Cheetah-like Cat *Miracinonyx inexpectatus* of North America, *J. Vertebr. Paleontol.*, 1990, vol. 10, no. 4, pp. 434–454.

Van Zyll de Jong, C.G., A Systematic Review of the Nearctic and Neotropical River Otters (Genus *Lutra*, Mustelidae, Carnivora), *Life Sci. Contr. Roy. Ontario Mus.*, 1972, no. 80.

Vangengeim, E.A. and Zazhigin, V.S., Faunal Assemblages and Faunas of the USSR: A Review, *Stratigrafiya SSSR. Chetvertichnaya sistema. Polutom 1* (Stratigraphy of the USSR, Quaternary System, Semivolume 1), Moscow: Nedra, 1982, pp. 267–279.

Vekua, A.K., *Kvabebskaya fauna akchagyl'skikh pozvonochnykh* (The Kvabebi Fauna of Akchagylian Vertebrates), Moscow: Nauka, 1972.

Viret, M.J., Les loess a bancs durcis de Saint-Vallier (Drôme) et sa faune de mammifères villafranchiens, *Nouvell. Arch. du Mus. d'Hist. Natur. de Lyon*, 1954, vol. 4, pp. 1–200.

Werdelin, L. and Solounias, N., The Hyaenidae: Taxonomy, Systematics, and Evolution, *Fossils and Strata*, 1991, no. 30.

Willemsen, G.F., *Mustella, Enchydrictis* (Carnivora, Mustelidae) from Tegelen (the Netherlands), *Proc. Ned. Akad. V. Weten*, 1988, vol. 91, no. 3, pp. 311–320.

Willemsen, G.F., A Revision of the Pliocene and Quaternary Lutrinae from Europe, *Scripta Geol.*, 1992, no. 101.

Wolsan, M., Évolution des carnivores quaternaires en Europe Centrale dans leur contexte stratigraphique et paléoclimatique, *L'Anthropologie, Paris*, 1993, vol. 97, no. 2/3, pp. 203–222.



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