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Carnivora of the Tamanian faunal unit (the Azov Sea area)

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ABSTRACT

The Carnivora assemblage of the Tamanian faunal unit (1.1–0.8 Ma) from the south of European Russia (Taman' Peninsula and southern shore of the Taganrog Gulf of the Azov Sea) is described. It contains five species: *Canis tamanensis*, *Canis (Xenocyon) lycaonoides*, *Lutra simplicidens tamanensis*, *Pachycrocuta brevirostris*, and *Homotherium latidens*. The Tamanian otter shows a more primitive condition than the Middle Pleistocene European *L. simplicidens* and its subspecific status is defined. *C. tamanensis* resembles the European *Canis mosbachensis* but shows very peculiar characteristics of the lower carnassial in the type specimen. In general, the Tamanian assemblage is composed of the elements that are characteristic of the post-Villafranchian carnivore fauna of Western Europe.

1. Introduction

The Tamanian faunal unit was distinguished by Gromov (1948) and placed between the Psekups and Tiraspol faunal complexes in the stratigraphic scale of continental deposits of southern Russia. The type assemblage of large mammals of the Tamanian faunal complex is the fossil fauna of the Taman' Peninsula, which was found in the sites of Kuchugury, Fontalovskaya, and Tsymbal, and in the type locality of Sinyaya Balka (Vereshchagin, 1957). The most characteristic elements of this complex are *Archidiskodon meridionalis tamanensis* Dubrovo and *Elasmotherium caucasicum* Borissjak.

The Tamanian fauna is correlated with the biozone of *A. meridionalis tamanensis* and characterizes the post-Villafranchian part of the European Early Pleistocene (Vangengeim et al., 1991). According to the geological, paleontological and paleomagnetic records, the time span of the Tamanian faunal assemblage was defined as 1.1–0.8 Ma, whereas the age of the type locality of Sinyaya Balka was biometrically evaluated as 0.95 Ma, based on the morphology of elephantine molars (Pevzner and Vangengeim, 2001).

The Tamanian Carnivora have not been revised since their first description by Vereshchagin (1957). Clearly, the old collections and newly collected materials badly require a revision and analysis. In the Taman' Peninsula, the Carnivora remains are known from the sites of Sinyaya Balka, Tsymbal, and Akhtanizovskaya (Fig. 1).

The locality of Sinayay Balka has been under study since 1912. The fauna originates from mudflow deposits. Carnivora remains were found in association with bones of other mammals. Particularly abundant are remains of elephants. More than 1000 specimens were recovered. The assemblage contains *Canis tamanensis*, *A. meridionalis tamanensis*, *Equus* aff. *sussenbornensis*, *E. caucasicum*, and *Bison* sp. (Vereshchagin, 1957). Remains of *C. tamanensis* Vereshchagin are represented only by the type specimen.

In the locality of Tsymbal, the fossiliferous beds are underlain by the Lower Kujalnik sands and covered by loess formation. There is a long list of small and large mammals including the index forms *A. meridionalis tamanensis* and *E. caucasicum*. Vereshchagin (1957) referred the Carnivora material from this site to *C. tamanensis* (upper P3) and to *Panthera* sp. (right ulna). Unfortunately, we have not had the opportunity to examine these fossils. According to the original description by Vereshchagin (1957: 25–26, Fig. 6), the P3 is too large for *C. tamanensis* ($L = 14.4$) and the ulna resembles *Homotherium*, rather than *Panthera*.

A right ramus of *Pachycrocuta brevirostris* was recently collected at the Akhtanizovskaya site. Tesakov (2004) studied a rich assemblage of small mammals from the same locality. The rodent fauna contains *Allophaiomys* cf. *pliocaenicus*, *Prolagurus (Lagurodon) arankae*, *Prolagurus (Prolagurus) pannonicus*, *Mimomys pusillus*, *Mimomys intermedius* and other forms. This assemblage is characteristic of the middle stage of the Tamanian faunal unit, local zone MQR8, and can be correlated with the Early Bicharian of Western Europe (Tesakov, 2004).

The Tamanian fauna of large and small mammals was also expanded by material from the adjacent territory on the southern shore of the Taganrog Gulf of the Sea of Azov. Sections of the 30 m high sea cliff are exposed near the villages of Port-Katon, Chumbur Kosa, Margaritovo, and Semibalki. They are composed of two lithostratigraphic sequences represented by lagoon clays and silts at the base and loess–palaeosoil series at the top. Finds of the

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Nomenclature

AMZ	Azov Museum-reserve, Azov, Russia
IQW	Senckenberg Institute, Department of Quaternary Paleontology, Weimar, Germany
GIN	Geological Institute of the Russian Academy of Sciences, Moscow, Russia
PIN	Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia
PIV	Paleontological Institute of the University of Vienna, Austria
ROMK	Rostov Museum of Regional Studies, Rostov-on- Don, Russia
L	length
W	width
D	depth
H	height
al	alveolus
tr	trigonid
tal	talonid; all measurements are in mm.

Tamanian mammals originate from the lagoon deposits exposed at the very base of outcrops (Dubrovo and Alexeev, 1964; Markova, 1990). According to paleomagnetic measurements, the fossiliferous layers in Port-Katon and Margaritovo belong to a reversely magnetized interval assigned to the upper part of the Matuyama Chron (Velichko et al., 1983; Tesakov et al., 2007). The Tamanian small mammal assemblages from Port-Katon were described by Markova (1990) and from Semibalki-3 by Rekovets (1994).

The studied Carnivora material comes from the localities of Margaritovo, Semibalki-3, and Chumbur Kosa (Fig. 1). In Margaritovo, a fragment of a right mandibular ramus of the large canid *Canis (Xenocyon) lycaonoides* was found together with remains of *A. meridionalis tamanensis*, whereas in Chumbur Kosa a jaw of *Lutra simplicidens* associates with remains of *Archidiskodon* sp.

The Semibalki-3 locality yielded remains of *A. meridionalis tamanensis*. The lower jaw of the saber-toothed cat *Homotherium* cf. *crenatidens* was described by Bajgusheva (2000) from this site. Besides, the list of macromammalian fauna of Semibalki-3 includes *Trogontherium cuvieri*, *Pachycrocuta* cf. *brevirostris*, *Equus major*, *Eucladoceros* aff. *orientalis*, and *Bison tamanensis* (Bajgusheva et al., 2001).

Fig. 1. Map of carnivore localities of the Tamanian fauna. 1 – Port-Katon, 2 – Semibalki-3, 3 – Chumbur Kosa, 4 – Margaritovo, 5 – Tsymbal, 6 – Akhtanizovskaya, 7 – Sinyaya Balka.

The Tamanian fauna of small mammals in the Semibalki-3 section is represented by *Clethrionomys glareolus*, *Prolagurus pannonicus transylvanicus*, *M. pusillus*, *M. intermedius*, *Allophaiomys pliocaenicus* and *Microtus hintoni* (Rekovets, 1994).

As mentioned above, the Tamanian Carnivora were described from the Sinyaya Balka, Tsymbal, and Semibalki-3 sites (Vereshchagin, 1957; Bajgusheva, 2000). The materials from Akhtanizovskaya, Margaritovo, and Chumbur Kosa have never been studied before. Analysis of new materials together with a revision of old collections allows the knowledge of the Carnivora assemblage of the Tamanian faunal complex to be expanded.

The studied material is stored at the Azov Museum-reserve Studies, Geological and Paleontological Institutes of the Russian Academy of Sciences.

2. Systematic palaeontology

Carnivora
Canidae Gray, 1821
Canis Linnaeus, 1758
C. tamanensis Vereshchagin, 1957
Fig. 2C, D and E.
Material: right mandibular ramus with p4–m2, with damaged anterior part and processes. Type specimen of *C. tamanensis*, PIN 1249/621
Locality: Sinyaya Balka
Age: late Early Pleistocene (Tamanian Faunal Unit)

Description and comparison. The partial mandible of a relatively small adult *Canis* with the straight toothrow at the juncture of the p4 and m1. In lateral view the paraconid top of the m1 is slightly higher than the top of the main cusp of the p4. The p4 has a very small second accessory posterior cusp, which is well separated from the prominent posterolingual cingulum. The structure of the m1 is very peculiar. Its protoconid has a posterior crest situated centrally instead of being lingually directed. Likewise, the metaconid is placed centrally, rather than lingually. The latter cusp is posteriorly appressed to the entoconid and separated from it only by a groove instead of being widely spaced. The hypoconid has a typical morphology with well-developed anterior and posterior crests. A transverse crest occurs between the hypoconid and entoconid. The talonid basin is abnormally small, the hypoconulid basin is well developed. The prominent cingulum encircles the talonid lingually. The relatively large m2 has a protoconid significantly smaller than the metaconid, the anterobuccal cingulum is well developed, the hypoconid is large, and the talonid basin is closed posterolingually by the entoconid ridge. There is no trace of the root of the m3 just behind the crown of the m2. The comparison below is based only on the normal part of dentition of *C. tamanensis*. The studied lower jaw is clearly smaller than in the living *Canis lupus*. Its depth behind the m1 ($D = 21.8$) is in the range ($D = 21.0$–25.0) of the individual population of *Canis mosbachensis* from the synchronous Untermassfeld fauna. The measurements of the tooth series are: $L/W/H$p4 = 12.8/5.5/7.5; L/L tr/W m1 = 21.3/15.3/8.5; L/W m2 = 9.4/6.8. These teeth are generally smaller than in the Untermassfeld sample but come close to the minimum values of *C. mosbachensis* from other Pleistocene European localities. The size of the studied specimen is also close to *Canis arnensis* from the European Late Villafranchian.

C. tamanensis differs from *C. lupus* in smaller size, higher and straighter position of the p4 relative to the m1, occurrence of the posterior basal cingulum in the p4, just behind its second accessory cusp. All above mentioned features *C. tamanensis* share with the

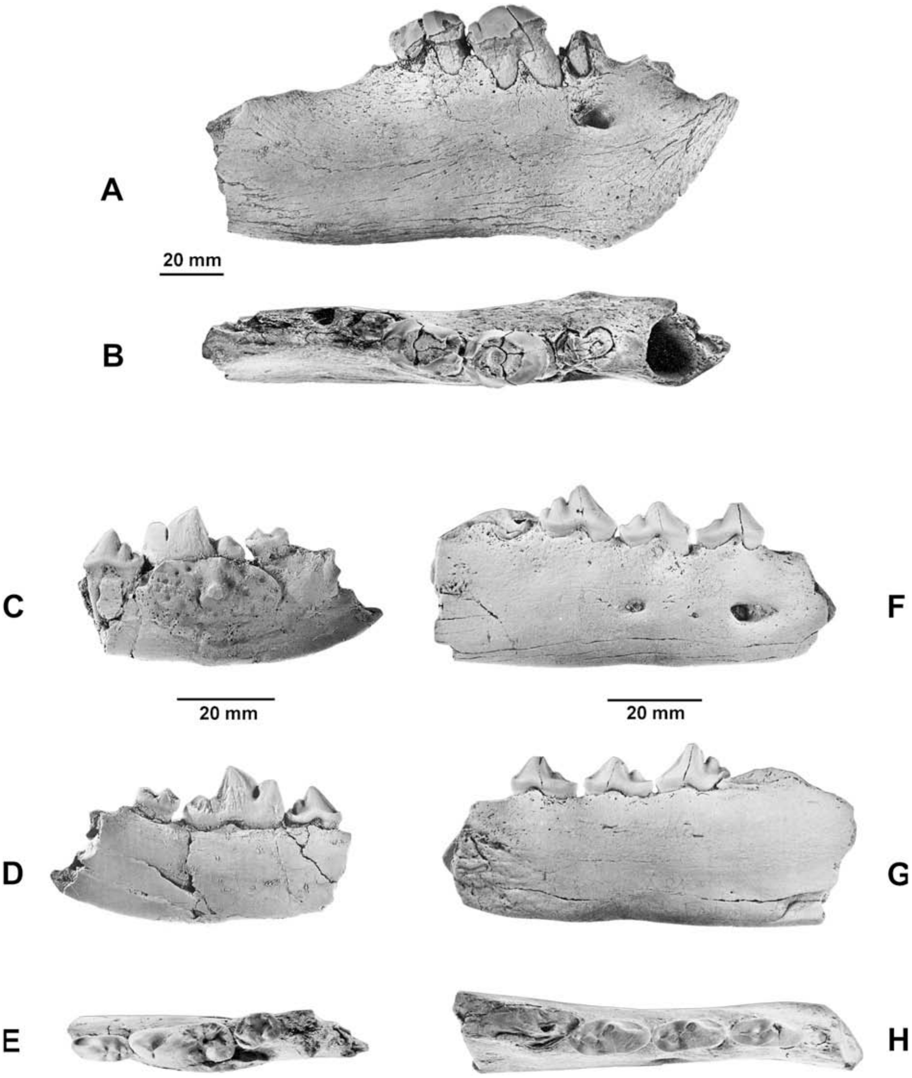

Fig. 2. *Pachycrocuta brevirostris*, GIN 1126/1, Akhtanizovskaya: A – lateral view, B – occlusal view. Scale bar 20 mm. *Canis tamanensis*, PIN 1249/621, Sinyaya Balka: C – lateral view, D – lingual view, E – occlusal view. Scale bar 20 mm. *Canis (Xenocyon) lycaonoides*, GIN 1125/1, Margaritovo: F – lateral view, G – lingual view, H – occlusal view. Scale bar 20 mm.

group of the Pliocene to Early and Middle Pleistocene canids, like *Canis etruscus*, *C. arnensis*, and *C. mosbachensis*. It differs from the Villafranchian forms, *C. etruscus*, and *C. arnensis*, in a slightly lower position of the p4 relative to the m1, a more backward sloping of the anterior margin of the m1, and a more differentiated size of the protoconid and metaconid in the m2. *C. tamanensis* fits well the characteristics of *C. mosbachensis* in having a moderately elevated p4 relative to the m1 and a moderately sloped anterior vertical border of the m1.

Discussion. Vereshchagin (1957) erected a new species, *C. tamanensis*, on the basis of the incomplete lower jaw PIN 1249/621 from Sinyaya Balka. He pointed to a similarity of the new form with the *Cuon-Lycaon* group of extant canids due to a lack of m3. However, Vereshchagin (1957) considered the Tamanian canid within the genus *Canis* because of the presence of a complete set of talonid cusps in its m1.

The present examination of the type specimen of *C. tamanensis* indicates some affinities with the small European wolf, *C. mosbachensis*, from the late Early to early Middle Pleistocene. On the other hand, *C. tamanensis* demonstrates peculiar characters in the structure of the m1 and in incomplete lower dentition with a lacking alveolus of the m3. According to our data, a reduction of the m3 sometimes occurs among canids with a hypocarnivorous type of m1. For example, a single mandible without an alveolus of the m3 is present in the abundant material of *C. mosbachensis* from Untermassfeld (Sotnikova, 2001). However, the described morphology of the m1 is not recorded in living and fossil forms of Canini. Taking into account that the aberrant structure of the m1 is not seen in other fossil canids of this time interval, we propose to leave *C. tamanensis* unsynonymized until the additional material on the small wolf from this area is available.

C. (Xenocyon) lycaonoides (Kretzoi, 1938)
Fig. 2F, G and H
Material: fragmental right mandibular ramus with alveoli of p1 and m1, p2–p4 are present. GIN 1125/1
Locality: Margaritovo
Age: late Early Pleistocene (Tamanian Faunal Unit)

Description and comparison. The mandibular ramus belongs to a large canid that is similar in size to *C. lupus* and *C. (X.) lycaonoides*. The premolar row is not medially bent as in *C. lupus*. The largest and anteriormost mental foramen lies below the anterior root of the p2, the smaller one is below the p3, whereas the smallest foramen is below the posterior root of the p2.

The teeth length in the row of p2-p4 shows a slight backward increase at about 1 mm per tooth. Lower premolars are not separated by a diastemata. The lower part of the crown of the p4 is somewhat elevated over the bases of the other premolars. The posterior cusps occur in all preserved premolars. Additionally, a tiny second accessory cusp, well separated from the posterior cingulum, is present in the p4.

The Margaritovo form differs from *C. lupus* in the straight toothrow, premolars with a primitively long talonid part, and the posterior second cusp of the p4 not fused with the cingulum. It shares with *C. (X.) lycaonoides* large dimensions, the straight toothrow, the higher position of the p4 relative to other premolars, a p4 with a tiny second accessory cusp separated from the posterior cingulum. The studied specimen differs from the majority of Middle Pleistocene samples of *C. (X.) lycaonoides* in having a p2 with the posterior accessory cusp and a long talonid part. Like the Epivillafranchian population of *C. (X.) lycaonoides* from Untermassfeld, the studied form has the posterior cusp of the p2, though the tooth is relatively longer and narrower.

The size of the horizontal ramus GIN 1125/1 is in the range of the Eurasian *C. (X.) lycaonoides* (see in Sotnikova, 2001, Table 17). The depth of the mandible (*D*) behind the p2 is 26.5, and 30.5 behind the p4. The alveolar length of p1-p4 is 53.0; *L*/*W* p2 = 14.1/6.2; *L*/*W* p3 = 15.0/6.5; *L*/*W* p4 = 16.4/7.7.

Discussion. The large canid *C. (X.) lycaonoides* was a common member of the post-Villafranchian mammalian communities in Eurasia. Its stratigraphic range spans the interval from the late Early to the Middle Pleistocene. Its distribution area stretched from England to Greece in Europe and from high latitudes of Siberia to Tajikistan and China in Asia. However, so far the available cranial material is insufficient for the understanding of its actual systematic and evolutionary position. The principal characteristics which define this taxon are the distinct hypercarnivorous trend in the structure of its upper and lower molars (M-m/1-2) and the presence of an m3 (Kretzoi, 1938; Schütt, 1974; Rook, 1994; Sotnikova, 2001).

The premolar morphology of this taxon is poorly known. The studied specimen has a p2 with a posterior accessory cusp, as in most specimens from the Untermassfeld sample. But, contrary to the German material, the Tamanian form has narrower and lower crowned premolars with more elongated posterior part. At present it is difficult to evaluate whether these differences are of species or population level. Therefore, we consider the Tamanian form within the widely distributed species *C. (X.) lycaonoides*.

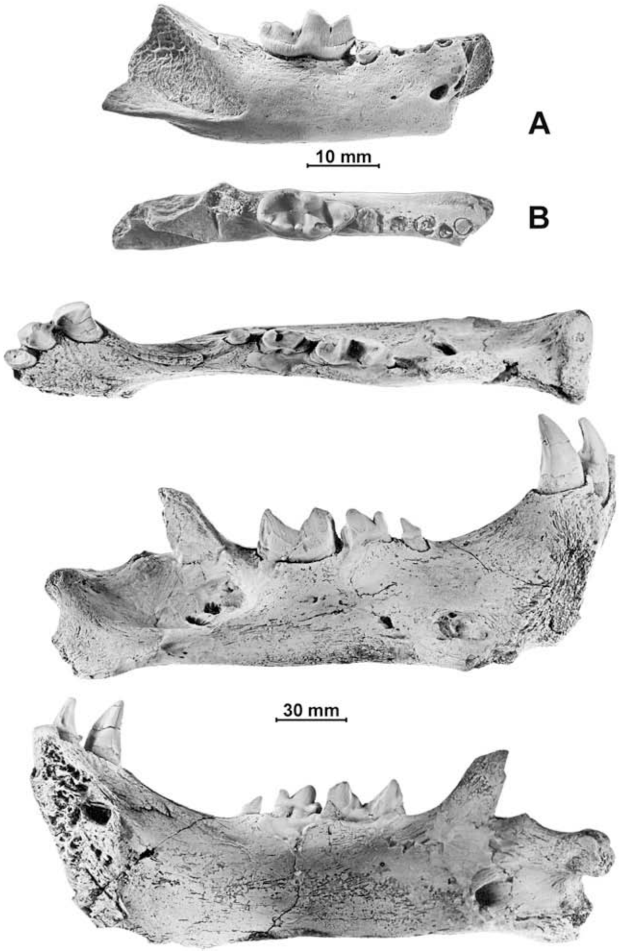

Fig. 3. *Lutra simplicidens* tamanensis, AMZ/OP-966, Chumbur Kosa: A – lateral view, B – occlusal view. Scale bar 10 mm. *Homotherium latidens*, ARM/OP-827, Semibalki-3: C – occlusal view, D – lateral view, E – lingual view. Scale bar 30 mm.

Mustelidae Fischer von Waldheim, 1817
Lutra Brunnich, 1772
L. simplicidens Thenius, 1965
Lutra simplicidens tamanensis Sotnikova ssp. nov.
Fig. 3A, B.
Holotype: incomplete left mandibular ramus with m1, posterior root and posterobuccal part of p4 crown, and alveoli of p2-3 and m2. All processes and incisor part are not preserved. AMZ: KP-27075/OP-966 (AMZ/OP-966 in the further description)
Locality: Chumbur Kosa, southern shore of the Taganrog Gulf of the Sea of Azov
Age: late Early Pleistocene (Tamanian Faunal Unit)
Etymology: in reference to the Taman' Peninsula
Differential diagnosis: lower carnassial differs from the m1 of nominative subspecies by a talonid width equal to that of the trigonid, a less enlarged metaconid, a less rounded posterior occlusal outline, complete number of well-developed cusps of the talonid blade.

Description and comparison. The studied mandibular ramus has a *Lutra*-like appearance. Its mandibular depth is lower than the length of the m1. There are three mental foramina aligned obliquely downward from the p2 to the p4. The first is below the p2, the largest is below the p3, and the smallest, below the anterior root of the p4. The deep masseteric fossa is expanded to the level of the posterior margin of the m1. The toothrow is relatively straight. The posterior part of the p4 crown does not overlap the anterior margin of the m1. The p2 is two-rooted with the anterior root shifted outwards. The anterior part of longitudinal axis of the p3 slightly diverges buccally, contrary to the p4, which has the long axis parallel to that of the mandible. There is a long diastema between the m1 and the root of the m2.

Morphologically the lower carnassial has an overall similarity to the m1 of the river otter. Its trigonid and talonid are equal in width, contrary to a broader talonid in *Lutra lutra* and a broader trigonid in *L. simplicidens simplicidens*. The metaconid is a relatively large cusp. The metastylid is present and placed directly behind the metaconid. Two distinct grooves separate it from the hypoconid and metaconid. The hypoconulid is present and aligned with the hypoconid. The prominent lingual rim closes the shallow talonid basin from the inner side. The buccal cingulum is incomplete with a well-developed anterobuccal cingulum encircling the paraconid and the prominent buccal cingulum that extends around the hypoconid and hypoconulid of the m1. In *L. lutra*, the anterobuccal and buccal cingula form a strong continuous cingulum.

The studied m1 differs from *L. lutra* in the talonid width matching the trigonid one, the posterior occlusal outline is rounder, the metaconid larger, the talonid basin shallower, an incomplete buccal cingulum, and a more prominent lingual rim around the talonid. Besides, the premolar row of AMZ/OP-966 has a more linear arrangement of p2-p4 in the horizontal plane of the mandible contrary to the more curved condition in *L. lutra*.

The Tamanian otter shares with the type specimen PIV/VII-36 of *L. simplicidens* the following features: the more linear arrangement of the premolars, the carnassial with a large metaconid, a shallow talonid basin and an incomplete buccal cingulum. Its m1 differs from the carnassial of *L. s. simplicidens* in a somewhat longer talonid with a more elliptic form of the posterior occlusal outline and in a well-developed hypoconulid and metastylid. Comparative mandibular measurements are given in Table 1.

Discussion. The known Late Pliocene record of otters in Europe is very scarce and fragmentary. Some isolated remains were recorded from Middle Villafranchian localities of Western Europe (Willemsen, 1992). In addition, a *Lutra*-like ramus without teeth was recently described from Liventsovka, MN17, Russia (Sotnikova et al., 2002). Early Pleistocene finds of *Lutra* are not known in Europe.

Thenius (1965) proposed a new species *L. simplicidens* based on the incomplete mandible with a p2-p3 and an m1 and partial postcranial elements from the Middle Pleistocene locality of Hundsheim (Deutsch-Altenburg), Austria. According to Thenius, the new species is distinct from the extant *L. lutra* in some morphological characteristics of the m1, different proportions of lower premolars, and more specialized limb bones.

Willemsen (1992) summarized the data on the species and included some additional fossil material previously referred to the genus *Lutra*. This material is represented by partial mandibles and postcranial elements from the Middle Pleistocene localities Voigtstedt, Süssenborn, Mosbach, East Runton, and West Runton. According to the amended diagnosis given by Willemsen (1992), *L. simplicidens* is characterized by "p2-p3 broader than in *L. lutra*, m1 with short and narrow talonid and larger metaconid compared to *L. lutra*, no hypoconulid, hypoconid is a ridge forming the outer border of the rather flat talonid, inner cingulum only present at the anterior basis of the paraconid".

The diagnosis stresses that the important distinction between the living *L. lutra* and fossil *L. simplicidens* is in the weakening of the carnassial function in the dentition of the latter form. This is expressed in a broadening of premolars and trigonid of the m1, a flattening of the talonid basin, and increasing of the metaconid and lingual talonid rim in the m1.

According to Van Zyll de Jong (1972), the fossil Lutrinae show the two main types of dentition. These are correspondingly the cutting (primitive condition) and the crashing (advanced condition) specializations. The latter adaptation could have originated recurrently from the more primitive condition in different lineages, including those referred to the genus *Lutra*.

Our comparison shows that the Tamanian otter is more similar to *L. simplicidens* than to *L. lutra*. It, however, retains more carnivorian features in the structure of the m1 than at L. s. simplicidens. Compared to Middle Pleistocene samples of *L. s. simplicidens*, the studied form has an m1 with a less rounded posterior margin of the talonid basin, a smaller metaconid and a more complicated talonid blade. The talonid of the type specimen of *L. s. simplicidens* from Hundsheim has a most simplified morphology with lacking metastylid and hypoconulid. In contrast, in the talonid of the studied form these cusps are well expressed. The description given by Willemsen shows that a metastylid in the m1 is present in the Voigstedt, Mosbach, East and West Runton samples. The hypoconulid can occur as well, as seen in the m1 from Mosbach. The presence of the complete number of cusps of the talonid blade points to the more cutting condition in the m1 of the living *L. lutra*. Hence, the complex structure of the talonid blade is likely a common character of the cutting adaptation in the m1 of the river otter. This character can be regarded as a basal type for the genus.

Table 1
Comparative mandibular measurements of *Lutra simplicidens*.

	Chumbur Kosa	Hundsheim[a]	E. Runton[a]	W. Runton[a]	Mosbach[a]	Voigstedt[a]
	AMZ	PIV	BM	CM	SMF	KMBF
	OP-966	Hsh VIII/26	6089	CR4. 984	PA/F 8718	I-711 K
D behind m1	13.3	–	–	–	–	–
D between p4–m1	11.4	13.1	13.7	–	–	–
L p2–m2 al.	34.9	33.9	32.3	–	–	–
L p2 al.	3.2	–	2.8	–	–	–
L p3 al.	5.5	–	5.9	–	–	–
L p4 al.	6.9	–	7.2	–	–	–
L m1	13.1	12.8	12.0	12.7	12.9	12.5
L m1tr.	8.2	–	6.8	7.1	8.0	7.5
W m1tr.	6.7	–	6.1	6.3	6.6	6.1
W m1tal.	6.7	–	5.9	6.1	6.3	5.9

[a] Measurements after Willemsen (1992).

The Tamanian form is the earliest among otters of the simplicidens group. It demonstrates a more primitive stage of cutting adaptations. It is evident now that the lineage of *L. simplicidens* evolved from more carnivorous forms, apparently with a *L. lutra*-like type of m1, through more advanced forms, like *L. s. tamanensis*, and finally to the derived type of the Middle Pleistocene otter, *L. s. simplicidens*. Actually, the *L. s. simplicidens* from Hundsheim and from other localities of Western Europe is more advanced than the Tamanian otter in a somewhat broader m1, a larger and higher metaconid of the m1, a relatively short, round and shallow basined talonid, simplified talonid blade (Fig. 4). Thenius (1965) pointed out that the Hundsheim otter is not a direct ancestor of the living river otter because of its very specialized postcranial skeleton. The studied trend in the development of the lower carnassial characters in the two subspecies of *L. simplicidens* supports Thenius' opinion that the extant *L. lutra* and Early–Middle Pleistocene group of the fossil otters are only remotely related.

Hyaenidae Gray, 1869
Pachycrocuta Kretzoi, 1938
P. brevirostris (Aumard, 1846)
Fig. 2A, B
Material: part of the right mandibular ramus with alveoli of canine and m1, root of p2 and p3–p4. All processes are not preserved. GIN 1126/1
Locality: Akhtanizovskaya
Age: late Early Pleistocene (Tamanian Faunal Unit)

Description and comparison. The studied specimen with a very large horizontal ramus and worn main cusps of the p3–4 belongs to an adult individual. Its morphological characters are typical of *P. brevirostris* in every respect. The mandible is massive and high in the horizontal ramus with one, large mental foramen below the p2. A very high symphysis portion extends to the level of the middle of the p2 crown. The toothrow is relatively straight. The p3 is more robust than the p4. It has a large posterior accessory cusp and lacks the anterior one. The three-cusped p4 has a posterolingual cingulum not lingually enlarged.

The alveolar length of the p2–m1 = 95.3; the mandibular depth between the p3 and p4 = 58.0; the same depth anterior to the p2 = 59.0; the alveolar length of the c = 26.1, of the p2 = 18.0, of the m1 = 28.9; the size of the p3 and p4 are: L/W p3 = 26.2/18.8, L p4 ca. 26.2.

The dimensions of the studied specimen fit well with the Eurasian samples of *P. brevirostris* reported by Howell and Petter (1980), Koufos (1992), and Turner and Antón (1996). Our specimen is, however, closer to the upper limit of the reported size range.

Discussion. The large *P. brevirostris* was a typical member of the Early and Middle Pleistocene faunal assemblages of Eurasia. Its wide dispersion begins at the base of the Late Villafranchian. Traditionally, its appearance in the Late Villafranchian was

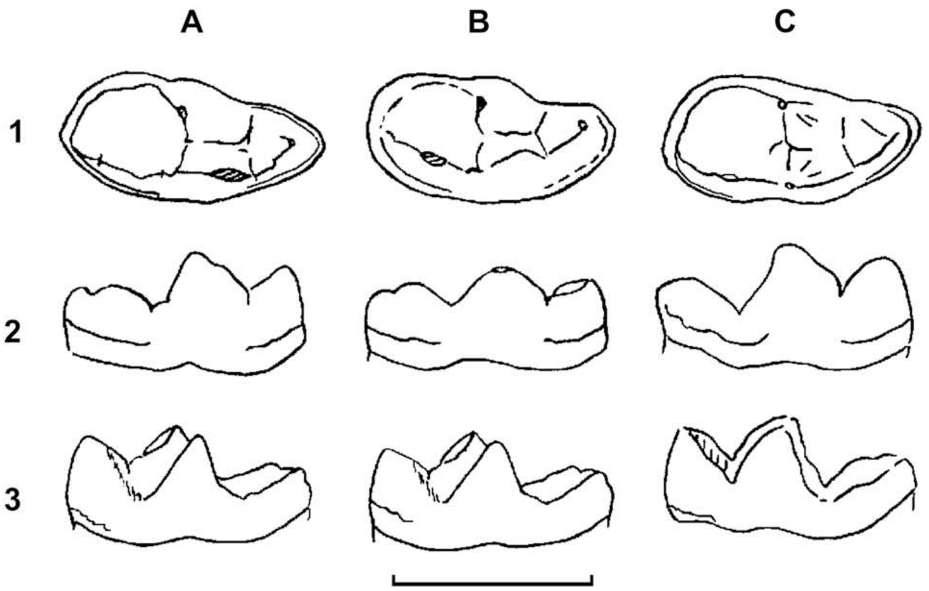

Fig. 4. The lower carnassial of *Lutra simplicidens:* A – *Lutra simplicidens tamanensis*, Chumbur Kosa, ARM: KP-27075/OP-966; B – *Lutra simplicidens simplicidens*, Mosbach, after Willemsen (1992); C – *L. s. simplicidens*, Hundsheim, after Thenius (1965); 1 – occlusal view; 2 – lateral view; 3 – lingual view. Scale bar 10 mm.

considered to be one of the major biochronological events in the history of West European mammals (Torre et al., 1992). However, recent studies indicate that the "*Pachycrocuta*-event" is more diachronous with the earliest occurrences in the Late Pliocene of the Almenara-1 locality, Spain, and in the Liventsovka locality, MN17, Russia (Agusti and Moyà Solà, 1998; Sotnikova et al., 2002). Therefore, the FAD of *P. brevirostris* in Europe is dated to a level predating the Olduvai Subchon.

Our previous study traced some differences in the mandibular features of the *Pachycrocuta*. The morphotype of the m1 with a two-cusped talonid characterizes the Villafranchian forms, whereas the single-cusped talonid mostly occurred in post-Villafranchian samples of *P. brevirostris*. The increasing robustness of the premolars, the absence of anterior accessory cusps in the p2 and p3, together with the reduction of the talonid and decreasing number of talonid cusps is considered as an advanced trend in the development of *P. brevirostris* (Sotnikova et al., 2002). Unfortunately, the studied specimen bears limited information. Nevertheless, the absence of the anterior cusp on the p3 indicates a relatively derived condition of this form.

Felidae Gray, 1821
Homotherium Fabrini, 1890
Homotherium latidens (Owen, 1846)
Fig. 3C, D and E
Homotherium cf. *crenatidens*: Bajgusheva, 2000, p. 35, Fig. 5

Material: right mandibular ramus with i2-3, c1 and p3–m1, the posterior part of the coronoid process and the ventral border of the mental area are not preserved. Collection of AMZ: KP-26386/23, OP-827 (referred to as AMZ/OP-827 in the text below)
Locality: Semibalki-3 (layers 4–5)
Age: late Early Pleistocene (Tamanian Faunal Unit)

Description and comparison. The described ramus is directly compared with the *Homotherium crenatidens* from Kuruksay (MN17), and Liventsovka (MN17), and with the Epivillafranchian form from Untermassfeld. The data on other homotheres are from the literature.

The ascending ramus has a comparatively low coronoid process with its anterior margin placed close to the m1. The ventral border of the horizontal ramus is nearly straight under the cheek teeth and goes downward just anterior of p3 level, forming a relatively slight mental flange. The anterior margin of a moderately deep masseteric fossa does not reach the posterior end of the m1. The large mental foramen occurs below the posterior end of the diastema between the c1-p3. The mandibular length is 222.4 between the condylar process and incisors, and 79.0 between the condylar process and the posterior end of alveolus of the m1. The depth of the ramus is 48.3 between the condylar and angular processes, and 49.5 anteriorly to the alveolus of the p3. The other measurements are given in Table 2.

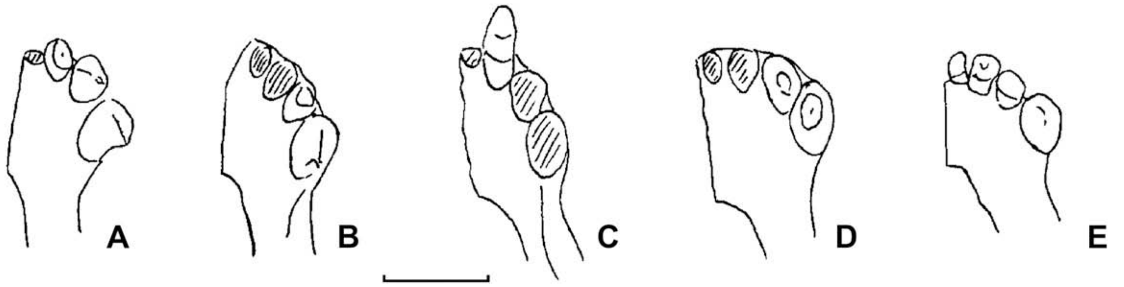

Fig. 5. The lower incisors–canine series in the different samples of *Homotherium*. Post-Villafranchian: A – *Homotherium latidens*, Semibalki-3, AMZ: KP-26386/23, OP-827; B – *Homotherium "crenatidens"*, Untermassfeld, after Hemmer (2001), C – *Homotherium ultimum*, Locality13 of Choukoutien, after Teilhard de Chardin (1939). Villafranchian: D – *H. nestianum*, Rocca Neyra, after de Bonis (1976); E – *H. crenatidens*, Seneze, after Ballesio (1963). Occlusal view. Scale bar 30 mm.

Table 2
Comparative mandibular measurements of different samples of *Homotherium.*

	Semibalki-3	Untermassfeld[a]		Liventsovka	Kuruksay
	AMZ	IQW	IQW	RRMOMK	PIN
	OP-827	1993/24372	1997/25985	RSU/94	3120/344
		(Mei. 23901)	(Mei. 25514)		
D behind m1	50.0	42.5	48.0	43.4	42.0
L of diastema c–p4	46.8	46.5	44.5	37.0	36.5
L i–m1 al	142.0	132.6[b]	129.0[b]	–	125.1
L c–m1 al	125.0	110.4[b]	109.3[b]	129.0	106.0
L p3–m1 al	64.0	62.0	–	72.0	55.0
L/*W* c	16.5/11.0	13.8/10.1	15.1/10.0	14.9/10.1	14.4/9.9
L/*W* p3	8.1/5.7	–	–	10.0/–	8.0/–
L/*W* p4	20.0/–	19.4/8.5	21.0/8.6	24.7/–	21.5/–
L/*W* m1	29.9/–	30.4/11.9	30.5/12.1	35.4/–	29.9/–

[a] Measurements after Hemmer (2001, Tab. 20).
[b] Measurements after Hemmer (2001, Plate 142).

The incisive portion of the dentition with transverse length (*L* i1-3 = 22.4) is arranged in a strong arc. Incisors and the canine are elevated relative to the cheek teeth. The third incisor has a ridge and basal tubercle on its lateral side, but lacks it on the mesial side, although the ridge with a short basal serration exists here. The roots of the i1-2 are laterally compressed with the length markedly greater than width: *L*/*W* i2 = 10.0/6.2, whereas the root of the i3 has almost equal anteroposterior and transverse diameters with *L*/*W* i3 = 11.0/11.5. The lower canine is stout, sharp, laterally compressed with finely serrated anterior and posterior ridges. The third premolar has a single root, a serrated, posteriorly directed principal cusp, and a weakly developed posterior cingular cusp. The p4 is worn and slightly broken posteriorly. It has a posteriorly directed crown with a well-separated anterior cusp and a reduced lingual cingulum. The crown of the p4 posteriorly slightly overlaps the anterior border of the m1. The very large carnassial shows worn blades and ventrally widened roots.

The Semibalki-3 specimen differs well from Villafranchian mandibles by the relatively smaller mental flange, a more anteriorly expanded coronoid process and less anteriorly expanded masseteric fossa, and smaller premolars with a weaker cingulum. In the studied specimen the mandibular flange begins more anteriorly than in the Kuruksay and Liventsovka samples. Incisors and the canine are arranged in an arc instead of a more transverse row, as seen in mandibles of Villafranchian homotheres from Rocca Neyra and Seneze (Figs. 5,6).

There are few mandibular samples of post-Villafranchian homotheres suitable for comparison. The material from the Epivillafranchian locality of Untermassfeld, which was described as *H. crenatidens* by Hemmer (2001), is especially close in size and morphology to the studied mandible from Semibalki-3. The studied form is similar to the specimen from Untermassfeld in its large size, the extremely arched incisors–canine series, moderately developed mental flange, placed just before the level of p3, and a well-separated anterior cusp of the p4. Both specimens share two very important features: a short masseteric fossa that reaches the posterior margin of the m1, and a coronoid process shifted more to the end of the toothrow. The Untermassfeld form differs from the Tamanian specimen by a very reduced p3 (Fig. 6I–J).

Another incomplete mandible, called *H. latidens*, is known from the Middle Pleistocene fauna of Hundsheim (Freudenberg, 1914). This form shares with a *Homotherium* from Semibalki-3 by the moderately developed mental flange, curved incisors–canine series, and a masseteric fossa expanded to the posterior margin of the m1 (Fig. 6G).

The anterior part of the horizontal ramus of *Homotherium* aff. *ultimum* was described by Foronova (1998) from the Sergeevo Suite, a Tamanian analogue in the Kuznetsk Basin (south of Western Siberia). This specimen resembles the Semibalki's homothere in a strongly arched incisors–canine series, premolar crowns clearly directed backward, and the anterior cusp of the p3 well separated from the main cusp. The Siberian form differs from the studied specimen in the p2 with a strong posterior cusp, and an incisors–canine series slightly elevated relative to the cheek teeth. These distinctive characters the Siberian homothere shares with the mandible, which was described by Scharapov (1989) as a new species *Homotherium teilhardipiveteaui* from the late Early Pleistocene locality of Lakhuti-2, Tajikistan. The latter form resembles the studied homothere in a relatively weak mental flange and a strongly arched incisors–canine series (Fig. 6K).

Comparison with the Chinese material from the Late-Middle Pleistocene localities 9 and 13 of Choukoutien (Teilhard de Chardin, 1936, 1939) shows the great similarity of European and Asian post-Villafranchian forms in strongly arched incisive and canine portion of the dentition, and a moderately developed mental flange (Fig. 6L).

Disscussion. The saber-toothed homotheres are well known throughout Europe and Asia in the extensive time interval of about 3.0 m.y. The FAD of this group in Europe is recorded in the fauna of Odessa Catacombs, and is correlated with the end of MN15 (Vangengeim et al., 1998). The last records are dated to 0.5 Ma in the sites from England, and Germany (Turner and Antón, 1997).

A number of different species have been included in the genus *Homotherium* in Eurasia. Among these are four widely recognized European species: *Homotherium nestianum* and *H. crenatidens* (Villafranchian), *H. latidens* and *Homotherium moravicum* (post-Villafranchian). Besides, *Homotherim davitašvlii* (Middle Pliocene of Georgia), *H. teilhardipiveteaui* (late Lower Pleistocene of Tajikistan), and *H. ultimum* (Lower-Middle Pleistocene of China) were recorded from the Caucasus and Asia (Teilhard de Chardin, 1936, 1939; Vekua, 1972; Scharapov, 1989).

Ficcarelli (1979) considered the distinctions between two Villafranchian species as an individual variability of a single species of *Homotherium* and synonymized *H. nestianum* and *H. crenatidens*. In contrast, Ballesio (1963) and de Bonis (1976) assigned these forms to separate species. In addition, Ficcarelli synonymized Asian *H. ultimum* under *H. latidens*, based on their close size and dental morphology.

New data of the rich assemblage of *Homotherium* were obtained from the Late or Latest Villafranchian locality of Incarcal (Crespia, Girona, Spain) (Ponds Moyà and Moyà Solà, 1992; Antón and Galobart, 1999). The sample of *Homotherium* from this site showed a high degree of variations in dental size and proportions. These variations were accounted for as the sexual dimorphism of a single species. Based on the range of this variation, Ponds Moyà and Moyà Solà (1992) were able to suggest the synonymy of *H. nestianum*, *H. latidens*, and *H. moravicum* with *H. crenatidens*. Turner and Antón (1997) showed a priority of the name *H. latidens* for the entire group of the Plio-Pleistocene Eurasian homotheres.

Thus, the recent discussion led to a decrease in the number of species of Eurasian homotheres. However, this discussion was mainly based on the Middle to Late Villafranchian samples of *Homotherium*, which apparently represent the same species. So far the insufficient knowledge of both post-Villafranchian species, *H. latidens* and *H. moravicum*, hampered their comparison with older forms. For example, the type series of *H. latidens* consists only of a canine and incisors described by Owen in 1846. Since that time, numerous isolated teeth and other fragmental materials from the Middle Pleistocene of Europe were traditionally assigned either to this species or to *H. moravicum*, which is based on the scanty material and had not been fully revised either.

According to Ficcarelli (1979), the separation between *H. crenatidens* and *H. latidens* is based on the smaller size and more curved and shortened upper canine of the latter form. All these features were originally used in the diagnosis of *H. latidens*. However, the

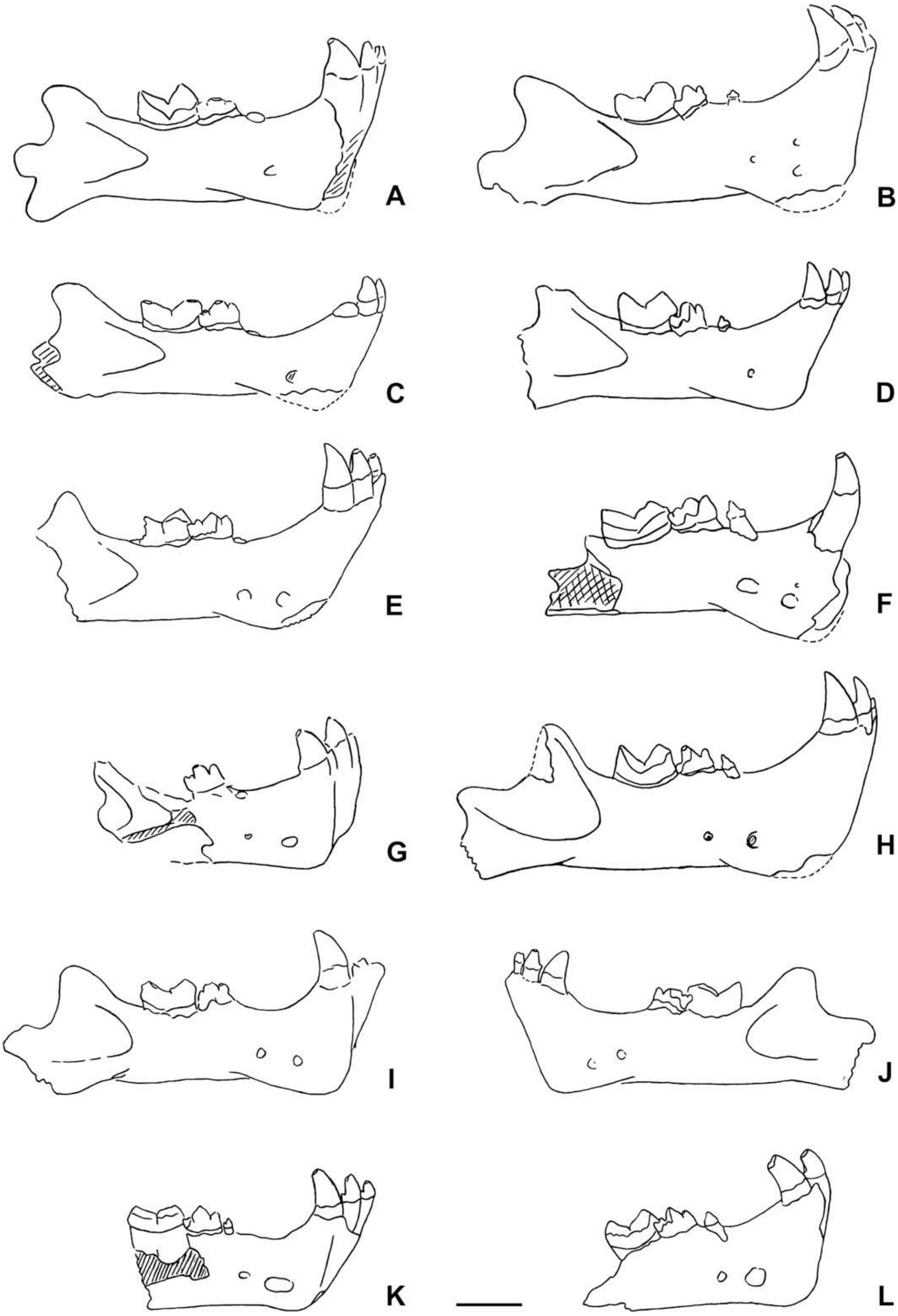

Fig. 6. The mandibles of different samples of *Homotherium*. A – *Homotherium crenatidens*, Seneze, after Ballesio (1963); B – *H. nestianum*, Rocca Neyra, after de Bonis (1976); C – *H. crenatidens*, Upper Valdano, after Ficcarelli (1979); D – *H. crenatidens*, Bugiulesti (Graunceanu), after Bolomey (1965); E – *H. crenatidens*, Kuruksay, after Sotnikova (1989); F – *H. crenatidens*, Liventsovka, after Sotnikova et al. (2002); G – *H. latidens*, Hundsheim, after Freudenberg (1914); H – *H. latidens*, Semibalki-3, AMZ/OP-827; I and J – *H. "crenatidens"*, Untermassfeld, after Hemmer (2001); K – *Homotherium "teilhardipiveteaui"*, Lakhuti-2, after Scharapov (1989); L – *Homotherium ultimum*, Locality 9 of Choukoutien, after Teilhard de Chardin (1936). Lateral view. Scale bar 30 mm.

high variability of these features became clear after the study of new materials of *Homotherium* from different sites in Eurasia, like Kuruksay, Liventsovka, Untermassfeld, Semibalki-3, and others. For example, the upper canine from Untermassfeld is comparable in size with the canine of the largest Villafranchian form *H. nestianum* from Rocca Neyra, whereas the upper canine of *H. crenatidens* from Kuruksay (MN17) is equal in size to the type specimen of *H. latidens* from Kent's Cavern, England (Hemmer, 2001, Tab. 21). The high degree of variation is also observed in the overall size of homotheres. On the other hand, the present analysis allows us to define species-level characteristics applicable to the distinction of the Villafranchian and later homothere forms. Our previous study allowed to assume a more complex Villafranchian history of the Eurasian *Homotherium* with at least two valid species: *H. davitašvlii* of the Lower Villafranchian, and *H. crenatidens* of the Middle to Upper Villafranchian (Sotnikova et al., 2002). The recent analysis shows that post-Villafranchian Europe and, likely, Asia witnessed an advanced form of *Homotherium*, which is distinct from the Villafranchian homotheres. Kurtén (1968), Ficcarelli (1979), and Bishop (1982) considered *H. crenatidens* to be a Villafranchian species and *H. latidens*, the younger form. These points of view and Owen's name *latidens* for the post-Villafranchian form are accepted here.

3. Conclusion

The Carnivora assemblage of the Tamanian fauna yielded remains of five species: *C. tamanensis*, *C. (X.) lycaonoides*, *L. s. tamanensis*, *P. brevirostris*, and *H. latidens*. Although poor in number of specimens and taxa, the Tamanian assemblage allows a number of clear biochronological conclusions.

The Tamanian assemblage contains the same elements as the post-Villafranchian Carnivora complex of Western Europe. Some new elements, which were unknown in Villafranchian times, appeared here. Among them are *C. (X.) lycaonoides*, *Lutra simplicidens*, and *H. latidens*.

During the late Early to Middle Pleistocene, two sympatric canids of different body size occurred in Eurasia. In the Tamanian assemblage they are represented by *C. tamanensis* and *C. (X.) lycaonoides*. As was shown by morphological analysis, *C. tamanensis* resembles post-Villafranchian *C. mosbachensis*, rather than the Villafranchian forms of similar size, *C. arnensis* and *C. etruscus*.

Lutra simplicidens is a member of the Middle Pleistocene Carnivora assemblage of Europe. It was identified in the Tamanian complex as well. The morphological characteristics of a new subspecies *L. s. tamanensis* demonstrate clearly a more primitive stage of development of the *L. simplicidens* lineage, apparently indicating the late Early Pleistocene age of the studied fauna. The partial skull of *Lutra* cf. *lutra* described by Vekua (1986) from the synchronous fauna of Akhalkalaki (Georgia) could belong to the same form.

The Tamanian *P. brevirostris* does not add any biochronological information due to its poor preservation. Rarely known in the Middle Villafranchian, this taxon was widespread in Eurasia since the Late Villafranchian to the end of the Middle Pleistocene.

H. latidens from Semibalki-3 shows characteristics that are also observed in the Untermassfeld form dated at about 1.0 Ma according to Kahlke (2000). Both specimens are considerably different from the older forms of the Middle and Late Villafranchian (Figs. 5 and 6).

Thus, the presence of *H. latidens* and *L. s. tamanensis* defines, respectively, the lower and upper stratigraphic limits of the Tamanian Carnivora community and allows us to correlate it with the post-Villafranchian part of the Lower Pleistocene. This conclusion is in good agreement with the age estimates of the Tamanian complex.

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