Pleistocene small porcupine from the Ural Mountains, Russia, with note on taxonomy of *Hystrix vinogradovi* (Rodentia, Hystricidae)

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ABSTRACT. The skull of the Pleistocene *Hystrix vinogradovi* found in Mokhnevskaya Cave in Middle Ural is examined. This find seems to be the northernmost fossil record of genus *Hystrix* in Europe. *H. vinogradovi* is similar to the Recent species, *H. (Acanthion) brachyura*, from South-East Asia in the characters of cranial morphology. Thus *H. vinogradovi* is considered to be a fossil subspecies of *H. brachyura: H. brachyura vinogradovi* comb. n.

KEY-WORDS: Hystrix, Pleistocene, Europe.

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Маленький дикобраз из плейстоцена Урала, Россия, с замечанием о систематическом положении Hystrix vinogradovi (Rodentia, Hystricidae)

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PEЗЮМЕ. Впервые изучен череп плейстоценового дикобраза *Hystrix vinogradovi*, найденный в Мохневской пещере на Среднем Урале. Находка является самой северной, из известных в Европе для рода *Hystrix*. По признакам краниальной морфологии *H. vinogradovi* сходен с современным видом *H. (Acanthion) brachyura* из Юго-Восточной Азии, что позволяет рассматривать его как подвид последнего, *H. brachyura vinogradovi* **comb. n.**

КЛЮЧЕВЫЕ СЛОВА: Hystrix, плейстоцен, Европа.

Introduction

The genus *Hystrix* is represented in the Europe by six fossil species: *H. parvae* (Kretzoi, 1951), *H. primigenia* (Wagner, 1848), *H. depereti* Sen, 2001, *H. refossa* Gervais, 1852, *H. etrusca* Bosco, 1898, and *H. vinogradovi* Argyropulo, 1941, as well as one extant species *H. cristata* L., 1758 (Sen, 2001). Weers (1994) assumed *H. refossa* and *H. etrusca* to be conspecific. The Late Pliocene – Holocene species (*H. refossa*, *H. vinogradovi*, *H. cristata*) are characterized by hypsodont cheek teeth, *H. vinogradovi* being of smaller size (Sen, 2001).

H. vinogradovi was described from the Binagady locality situated in environs of Baku in Azerbaijan (Argyropulo, 1941; Gromov, 1952). The geological age of the locality was preliminary determined as the Last Interglacial, Eem (Baryshnikov, 2002). Another small porcupine from the Early Pleistocene of Osztramos 8 in Hungary has been later described as a subspecies of this species, H. vinogradovi atavus (Janossy, 1972). The Late Pleistocene subspecies H. vinogradovi kudarensis was found in the caves Kudaro 1 & 3 in Georgia (Baryshnikov & Baranova, 1982).

Weers (1994) synonymized with *H. vinogradovi* the species *H. schaubi* Brunner, 1954 from the Late Pleistocene of the Fuchsloch Cave in Germany as well as

subspecies *H. cristata minor* Malez, 1963 from the Late Pleistocene of the Veternica Cave in Croatia. He also suggested that bone remains of the small porcupine from the Early Pleistocene of Rumania (Brassó) and Late Pleistocene of Moravia (Ostrov), Czech Republik (Podbaba), and Hungary (Kiskevélui Cave, Köháti Cave, Lambrecht Cave) may belong to *H. vinogradovi*. In the two localities, *H. vinogradovi* was revealed together with larger porcupines: *H. refossa* in Osztramos 8, Hungary (Janossy, 1972; Weers, 1994) and *H. indica* in Kudaro Caves, Caucasus (Baryshnikov & Baranova, 1982).

Position of *H. vinogradovi* among other representatives of the genus *Hystrix* seems to be uncertain. In the dimensions, it is similar to the Recent species *H. brachyura* L., 1758 from the southeastern Asia, which belongs to the subgenus *Acanthion* F. Cuvier, 1823. This allowed Weers (1994) to assume the affinity between *H. vinogradovi* and *H. brachyura* and provisionally include the former species to *Acanthion*, notwithstanding Janossy (1972) has rejected earlier that affinity. This uncertainty may be explained by the deficient information for the skull of *H. vinogradovi*.

The new material, which makes it possible to define more precisely the systematic position of *H. vinogradovi*, has been recently obtained during the commercial excavations in the Mokhnevskaya Cave in Middle Ural, Eastern Europe by the "Northwest" enterprise. This

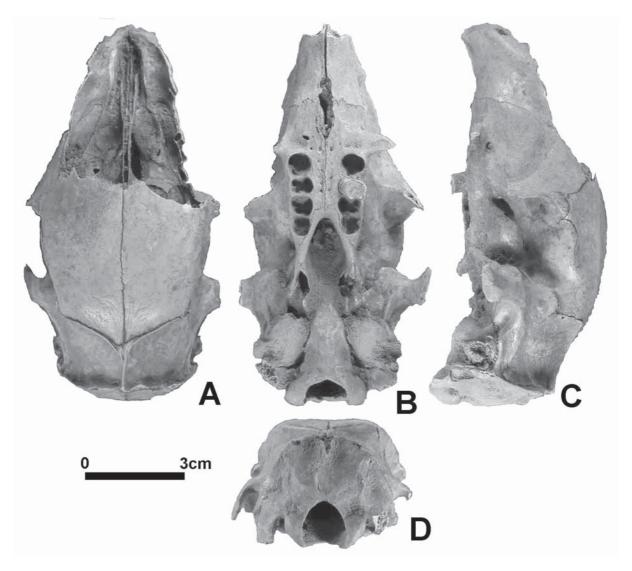


Figure 1. Skull of *Hystrix brachyura vinogradovi*, ZIN 87577 in dorsal (A), ventral (B), lateral (C), and caudal (D) views. Mokhnevskaya Cave, Perm Province, Russia; Late Pleistocene.

find seems to be northernmost record for the fossil porcupines in Europe. Two skull fragments, which are kept at the collection of Zoological Institute, Russian Academy of Sciences in Saint-Petersburg (ZIN), as well as the right humerus, were found there. The humerus greatest length from caput is 96.0 mm, distal breadth being 28.6 mm (Kosintsev & Podoprigora, 2003), that somewhat exceeds dimensions of this bone in *H. vino-gradovi* from Binagady (Gromov, 1952).

Below, on the basis of the cranial fossil remains from Mokhnevskaya Cave, the first description of the skull of *H. vinogradovi* is given.

Locality, material and methods

Mokhnevskaya Cave (=Makhnevskaya Ice Cave) is located in the Alexandrovskii District of Perm Province in Russia (N 59°26′, E 57°41′). A small porcupine has been excavated together with various Pleistocene mammal spe-

cies: Canis lupus, Ursus thibetanus permjak, Panthera spelaea, Mammuthus primigenius, Equus ferus, Cervus elaphus, Alces alces, and Bison priscus (Baryshnikov, 2001; Kosintsev & Podoprigora, 2003). Stratigraphic position of the locality is vague. However, a presence of thermophilous mammals as well as morphometric characteristic of horse teeth allow to ascribe this theriocomplex to the warm stage of the late Middle Pleistocene (OIS 7) or to the Last Interglacial (OIS 5e).

The porcupine remains comprise the almost complete skull without mandible (ZIN 87577) (Fig. 1) and maxillary fragment (ZIN 87578). In ZIN 87577, the nasal bones, zygomatic arcs, and arcs of infraorbital foramina are broken. The only tooth, left M1 is preserved. The bone tissue is dense and weakly fossilized, its color being yellowish brown. In ZIN 87578 the right P4 is present.

For comparison, three fossil cranial fragments of *H. vinogradovi* (ZIN 21918) from the type locality of Binagady in Azerbaijan and skulls of the Recent porcupines: *Hystrix (Acanthion) javanica* (F. Cuvier, 1823) (ZIN 10984, Java), *H. (Acanthion) brachyura subcristata* Swinhoe, 1870 (ZIN

Measurements, mm	Pleistocene	Recent					
	H. brachyura vinogradovi	H. brachyura subcristata	H. javanica	H. indica		H. cristata	
	ZIN 87577	ZIN 6632	ZIN 10984	ZIN 10978	ZIN 15810, ♀	ZIN 3049	ZIN 343, ♀
Total length	124.2	141.9	124.6	147.5	157.0	136.9	143.5
Basilar length	117.4	127.5	107.6	135.3	146.9	121.6	128.5
Length of the frontals	ca 50	30.1	35.0	41.0	44.0	26.8	28.9
Palatal length	64.2	73.2	59.4	74.8	84.3	67.4	74.2
Length of the diastema	39.0	38.6	31.5	42.5	49.1	36.0	39.4
Alveolar length P4-M3	28.3	30.0	24.8	32.4	33.9	32.1	34.5
Postorbital breadth	42.7	48.3	36.6	51.9	58.0	50.7	56.5
Zygomatic breadth	ca 71	75.0	60.4	80.9	86.2	72.8	ca 75
Occipital breadth	47.4	50.2	43.1	54.1	55.3	48.0	52.1
Height of the skull	46.0	56.6	42.3	59.6	59.3	50.1	63.7
Occipital height	36.4	39.7	34.9	39.5	43.2	37.2	40.3
Index (%)							
Frontal length/ Basilar length	42.6	23.6	32.5	30.3	30.0	22.0	22.5
Postorbital breadth/ Basilar length	36.4	37.9	34.0	38.3	39.5	41.7	44.0
Height/Basilar length.	39.2	44.4	39.3	44.0	40.4	41.2	49.6
Occipital height/ Occipital breadth	77.0	79.1	81.0	73.0	78.1	77.5	77.3

Table 1. Skull dimensions of fossil and recent *Hystrix*.

6632, Szechwan, China), *H.* (*Hystrix*) indica Kerr, 1792 (ZIN 10978, Transcaucasia; ZIN 15810, Turkmenistan), and *H.* (*Hystrix*) cristata L., 1758 (ZIN 343, zoo; ZIN 3049, Tunis) were examined.

Measurements generally taken in studying skulls in porcupines of the genus *Hystrix* (Weers, 1976, 1979, 1994) were used. Another 3 dimensions have been added: 1) total length – distance from the line connecting the posterior margins of the alveoli of the upper incisors to the apex of occiput (akrokranion), 2) occipital breadth — greatest distances between occiput sides at the base of paroccipital processes, 3) occipital height — distance from akrokranion to inferior border of the foramen magnum. Skulls and teeth were measured with dial caliper with accuracy 0.1 mm.

Description and comparison

Skull. The size of the ZIN 87577 specimen is small. The skull is relatively long, being less inflated as compared to those in species of the subgenus *Hystrix* s. str.

The nasal bones, which are generally treated to be diagnostic for the species of the genus *Hystrix*, are broken. Nevertheless, it is quite obvious that these bones were short and did not extend beyond the level of the orbital anterior margin (Fig. 1). In this character, ZIN 87577 is similar to *H. javanica* but diverges from species *H. indica* and *H. cristata*, possessing longer nasal bones. Within the extant porcupine species, *H. brachyura*, the subspecies *H. brachyura brachyura* L., 1758 demonstrates short nasal bones, whereas *H. brachyura subcristata* Swinhoe, 1870 has long nasal

bones (Weers, 1979). Consequently the fossil porcupine from Mokhnevskaya Cave resembles the former subspecies inhabiting the Malay Peninsula and Sumatra and Borneo islands and differs from the subspecies *H. brachyura subcristata* distributed in India, Indochina, and south China.

In the length of frontals, ZIN 87577 exceeds the species examined (see Tab. 1). The ratio of the frontal length mean to basilar length mean in *H. brachyura brachyura* does not surpass 35% (Weers, 1979). This ratio is still less in *H. brachyura subcristata*. Therefore, in this index, *H. vinogradovi* differs from both subspecies of *H. brachyura*.

The infraorbital foramen is large. The suture between maxillary and frontal bones is well distanced from the infraorbital foramen. The upper orbital margin is raised with regard of the skull roof, as in *H. javanica*, but not dropped, as in other examined species. The postorbital constriction is broad. ZIN 87577 is relatively broad in the level of zygomatic arcs. The suture between the frontal and parietal bones demonstrates a shape of narrow valley. It concurs with semicircular lines instead of crossing the skull, as in extant species. A distance between the frontal-parietal suture and the apex of occiput (akrokranion) is very minute (16.2 mm), being markedly shorter as compared to other species of the genus *Hystrix*. The sagittal crest is short.

The occiput is inclined forward, as a result the akrokranion being placed in front of the level of the occipital condyli (Fig. 1). The porcupines of the subge-

nus *Hystrix* s. str. and subspecies *H. brachyura subcristata*, demonstrate very similar location of the akrokranion. In contrast, in *H. javanica* and subspecies *H. brachyura brachyura* the occiput inclined backwards (Weers, 1979). In ZIN 87577, the occiput is broad, its height (from the lower margin of the foramen magnum) being markedly less than its greatest breadth that is characteristic of *H. cristata* and *H. indica*. The same shape and proportions of the occiput possesses ZIN 21918-3 from Binagady (occipital breadth 50.2 mm, occipital height 36.6 mm, ratio between height and breadth 72.9%). In ZIN 87577, the paroccipital processes are robust and directed downwards. Auditory bullae are inflated.

The skull is low, as in *H. javanica*. Choanas are narrow. The anterior margin of the palatal incision is wedge shaped, approaching forwards the level of the M2 alveolus. The other examined species demonstrate incision less expanding forwards. The palatine is narrow; therefore the upper cheek tooth rows are approximate one with another. Alveoli of the cheek teeth are large, the largest belonging to P4. The shallow pits are developed in front of the P4 alveoli. The diastema is long indicating that the rostral portion of the skull was relatively elongated (see Tab. 1).

In the alveolar length of the cheek tooth row P4–M3 in *H. vinogradovi*, ZIN 87577 (28.3 mm) and ZIN 87578 (28.7 mm) from Mokhnevskaya Cave are somewhat larger than ZIN 21918-1 and ZIN 21918-2 from Binagady (25.6 mm and 26.2 mm correspondingly). The both latter maxillary fragments show morphological characters similar to those of the Mokhnevskaya Cave porcupine: the distance between maxillary tooth rows is small, palatal incision extends forward approximately to the level of M2 alveolus, a pit is developed in front of P4, and the distance between frontal-parietal suture and occiput apex is short (ca 20.1 mm).

Cheek teeth. Only P4 and M1 are available for study.

P4 (occlusal length ca 8.5 mm, occlusal width 7.4 mm) in ZIN 87578 is partly broken. The tooth is heavily worn; four enamel islands present, no fold left. By the crown wear, it may be ascribed to the class G according to classification of Weers (1990). This tooth in the both specimens from Binagady shows the smaller occlusal measurements; ZIN 21918-1, left: length 6.5 mm, width 5.7 mm, and ZIN 21918-2, right: length 6.9 mm, width 5.5 mm (both class F). P4 from Mokhnevskaya Cave is also markedly larger than the teeth from Binagady.

M1 (occlusal length 7.0 mm, occlusal width 7.6 mm) in ZIN 87577, being measured from lingual side, demonstrates the crown height 4.8 mm; five enamel islands present; and no fold left (class G of Weers, 1990). The younger individuals of *H. vinogradovi* from Binagady possess following occlusal dimensions of M1: ZIN 21918-1: length 6.1 mm, width 5.9 mm (class E of wear), and ZIN 21918-2: length 6.8 mm, width 5.9 mm (class F of wear). Similar sizes were recognized for the *H. vinogradovi* teeth from Kudaro 1 & 3 Caves in Caucasus (Baryshnikov & Baranova, 1982).

In the size and ratio between the width and length, the examined cheek teeth of *H. vinogradovi* correspond to those of the Recent *H. brachyura* of the same degree of wear (Weers, 1990). The only exception is the larger P4 from Mokhnevskaya Cave.

Discussion

Distribution in former USSR. The survey of finds of *H. vinogradovi* in the Soviet Union territory has been published by Baryshnikov & Baranova (1983). *Hystrix* sp. described on the basis of the isolated teeth from the Early Pleistocene of the Tarkhankut in Crimea, Ukraine (Topachevsky, 1973) has been attributed to this species. The fossil remains of *H. vinogradovi* were recorded in the Middle and Late Pleistocene localities of Kudaro 1 Cave, Kudaro 3 Cave, and Binagady in Transcaucasia (Gromov, 1952; Baryshnikov & Baranova, 1982). Another find, the mandible with m1–m2 from the Late Pleistocene of Il'inka in south of Ukraine, was also ascribed to this species.

The specimens of *H. vinogradovi* found in the Mokhnevskaya Cave are the northernmost records of this species.

Beside the East European material, the maxillary fragment with M1 (occlusal length 7.4 mm, occlusal width 6.9 mm) from Late Pleistocene of the Razboinichiya Cave in Altai, which was regarded as *Hystrix* sp. (Ovodov, 2000), may be also attributed to *H. vinogradovi*. I.M. Gromov proposed a similar view (Gromov & Erbaeva, 1995).

Thus the distribution range of *H. vinogradovi* is mainly confined to Europe and Mediterranean, occurring over these borders in the south of Western Siberia (Fig. 2).

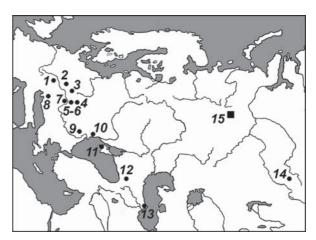


Figure 2. Map of the *Hystrix brachyura vinogradovi* records (according to data of Weers, 1994, with additions). Black quadrate indicates Mokhnevskaya Cave.

1—Fuchsloch Cave, Siegmannsbrunn, 2—Kotlarce, 3—Ostrov, 4—Osztramos 8, 5 — Kiskohat, 6 — Lambrecht Cave, Varebó, 7 — Csobánka near Budapest, 8 — Veternica Cave, Medvednica, 9 — Brassó, 10 — Il'inka near Odessa, 11 — Tarkhankut, 12 — Kudaro 1 Cave and Kudaro 3 Cave, 13 — Binagady, 14 — Razboinichiya Cave, 15 — Mokhnevskaya Cave.

H. vinogradovi was spread farther to the north as compared with other representatives of the genus. This porcupine seems to be less thermophilous. In the Caucasian caves of Kudaro 1 & 3, the fossil remains of H. indica and H. vinogradovi were recorded in the Middle Pleistocene layers, which have been formed in the warmer climate. At the same time, only H. vinogradovi remains were found in the Late Pleistocene layers formed in colder climatic conditions (Baryshnikov & Baranova, 1982).

Taxonomic status. The porcupines of the subgenera *Acanthion* and *Hystrix* s. str. are dissimilar in the spiny covering, however their cranial morphology gives no reliable diagnostic characters. This complicates the subgeneric attribution of *H. vinogradovi*. Nevertheless, in the small dimensions, elongated skull, and large infraorbital foramen, it is more closely related to species of the subgenus *Acanthion*, than to species of the subgenus *Hystrix* s. str.

The results of comparison confirm the idea of Weers (1994) on the affinity of *H. vinogradovi* with *H. brachyu-ra*. The taxon *H. vinogradovi* resembles the subspecies *H. brachyura brachyura* (in short nasal bones) as well as *H. brachyura subcristata* (in occiput shape). At the same time, *H. vinogradovi* differs from both the extant subspecies in the longer frontal bones, much more posterior position of the frontal-parietal suture, and relatively low occiput. Therefore, I accept the *H. vinogradovi* to be a fossil subspecies, *H. brachyura vinogradovi* comb. n.

This opinion may be reinforced by the remarkable coincidence of the Pleistocene distribution of *H. brachyura vinogradovi* in Europe and east Mediterranean region with that of the Asian black bear *Ursus thibetanus* G. Cuvier. The both taxa were found together in Kudaro caves in Caucasus and in Mokhnevskaya Cave in Ural Mountains (Baryshnikov, 2001). Presumably, *H. brachyura* and *U. thibetanus* inhabiting now forests of South-Eastern Asia simultaneously penetrated to Europe during warm stages of the Pleistocene.

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References

- Argyropulo A.J. 1941 [Rodents and insectivores of the Quaternary fauna of Binagady] // Priroda. No.3. P.88–91 [in Russian].
- Baryshnikov G. 2001. The Pleistocebe black bear (Ursus thibetanus) from the Urals (Russia) // Lynx (Praha). Vol.32. P.33–43.
- Baryshnikov G.F. & Baranova G.I. 1982. [On the finding of the Vinogradov porcupine in the Caucasian Paleolithic] // Trydy Zoologicheskogo Instituta AN SSSR. Vol.115. P.46–53 [in Russian].
- Baryshnikov G.F. & Baranova G.I. 1983. [Hystrix vinogradovi in the Pleistocene of Europe and Caucasus] // Gromov I.M. (ed.). [Rodents. Proceedings of the Sixth All Union Conference]. Leningrad: Nauka. P.39–41 [in Russian].
- Gromov I.M. 1952. [Fauna of the Pleistocene rodents (Rodentia) of Binagady and its nature] // Trudy Estestvenno-Istoricheskogo Museya Imeni Zardabi, Baku. T.5. P.203–349 [in Russian].
- Gromov I.M. & Erbaeva M.A. 1995. [The Mammals of Russia and Adjacent Territories]. Sankt Peterburg: Zoologicheskii Institut RAN. 522 p. [in Russian].
- Kosintsev P.A. & Podoprigora I.N. 2003. [The findings of porcupine *Hystrix vinogradovi* and Asian black bear *Ursus thibetanus* in Upper Pleistocene of Middle Ural] // Orlov V.N. (ed.). [Theriofauna of Russia and Adjacent Territories. Abstracts of the Seventh Meeting of the Theriological Society]. Moskva: Teriologicheskoe Obshchestvo. P.175 [in Russian].
- Ovodov N.D. 2000. [Fossil porcupine (*Hystrix* sp.) from Altai] // Drozdov N.I. (ed.). [Paleogeography of Stone Age. Correlation Between Environment and Archaeological Culture of Paleolithic in Northern Asia and Adjacent Territories]. Krasnoyarsk. P.100–102 [in Russian].
- Sen S. 2001. Early Pliocene porcupine (Mammalia, Rodentia) from Perpignan, France: a new systematic study // Geodiversitas. Vol.23. No.2. P.303–312.
- Topachevsky V.A. 1973. [Rodents of Taman Faunal Complex of Crimea]. Kiev: Naukova dumka. 236 p. [in Russian].
- Weers D.J., van. 1976. Notes on southeast Asian porcupines (Hystricidae, Rodentia). I. On the taxonomy of the genus *Trichys* Günther, 1877 // Beaufortia. Vol.25. No.319. P.15–31.
- Weers D.J., van. 1979. Notes on southeast Asian porcupines (Hystricidae, Rodentia). IV. On the taxonomy of the subgenus *Acanthion* F. Cuvier, 1823 with notes on other taxa of the family // Beaufortia. Vol.29. No.356. P.215–272
- Weers D.J., van. 1990. Dimensions and occlusal patterns in molars of *Hystrix brachyura* Linnaeus, 1758 (Mammalia, Rodentia) in a system of wear categories // Bijdragen tot de Dierkunde. Vol.60. No.2. P.121–134.
- Weers D.J., van. 1994. The porcupine *Hystrix refossa* Gervais, 1852 from the Plio-Pleistocene of Europe, with notes on other fossil and extant species of the genus *Hystrix* // Scripta Geologica. Vol.106. P.35–52.