Late Miocene – early Pliocene porcupines (Rodentia, Hystricidae) from south European Russia

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ABSTRACT. The revision of Anchitheriomys caucasicus (=Amblycastor caucasicus Argyropulo, 1939) from the early Pliocene (early Ruscinian, MN14) of Northern Caucasus resulted in its attribution to porcupines, rather than to beavers as was initially thought. This form from the Kosyakino sand pit represents a clear species of the porcupine genus Hystrix, H. caucasicus. The species shows affinities with the group of semihippsodont porcupines, H. primigenia (Wagner, 1848) (MN12-13) – H. depereti Sen, 2001 (MN15). In size it is larger than the former and close to the latter species. A well preserved P4 from the late Miocene (late Turolian, MN13) locality Morskaya 2 in the Azov Sea Region indicates the first record of H. primigenia in Russia.

KEY WORDS: Hystrix, Hystricidae, Rodentia, late Miocene, early Pliocene, Azov Sea Region, Northern Caucasus, Russia.

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Познанмнениеновые – ранненплиоценовые дикобразы (Rodentia, Hystricidae) юга европейской России

Introduction


Methods

The dental terminology follows Sen (2001) with additions. All measurements are in mm. The systematics of the genus Hystrix is after Weers (1994), Sen (2001) and Wang & Qiu (2002). The materials are housed in the collection of the Paleontological Institute of the Russian Academy of Sciences (PIN) in Moscow, Russia, and Taganrog State Pedagogical Institute (TSPI), in Taganrog, Russia.

Systematic Paleontology

Order Rodentia Bowdich, 1821

Family Hystricidae Fischer, 1817

Subfamily Hystricinae Fischer, 1817

Genus Hystrix Linnaeus, 1758

Hystrix caucasicus (Argyropulo, 1939)

Figs. 1, 2.

**Type locality.** Kosyakino sand pit, near the city of Stavropol, Stavropol Region, Northern Caucasus, Russia.

**Stratigraphic level.** Lower Pliocene, lower Ruscinian, MN14.

**Description.** A large porcupine. The p4 (the holotype) has three roots: one curved and grooved anterior and two posterior ones. The tooth is semihypsodont. Due to insignificant wear it likely represents a young age class. The occlusal surface is concave and rounded-rectangular in outline. There are a deep hypoflexid and four lingual synclinids. The hypostrid nearly reaches the base of the crown. On the edge of the posterolabial side of the protoconid there is a narrow exit from the anterolabial longitudinal enamel island, which is the detached outer part of the anterior mesoflexid (and it can be termed labial mesossettiid). Between the metaconid and metalophulid there is the small additional open flexid, which closely joins the anterofossettiid. Therefore, this fold should be defined as an anteroflexid, and its exit groove, an anterostrid. The lingual striids run about 1/3 (posterior mesostrid) and 1/4 (anterior mesostrid and anterostrid) of the crown.
height. The anterior mesoflexid connects to the posterior one in the middle of the occlusal surface. The mesolophid is stout. The posterior mesoflexid connects to the inner part of the hypoflexid. The posterofossisetid is divided into two parts by a short crochet issued from lingual part of posterolophid. The enamel walls of the inner part of the posterior mesoflexid and posterofossisetid are notched (not plicated).

**Measurements.** Occlusal length (L) 12.2, occlusal width (W) 9.0; crown base (maximum) length (LB) 14.5, crown base width (WB) 11.5; maximum enamel height (H) 13.0. The index of hypsodonty (H/L) 1.06. The index of robusticity (WB/LB) 0.793.

**Comparison.** *H. caucasia* differs from all post-Ruscinian *Hystrix* species in larger size (Fig. 5) and less developed hypsodonty. It differs from the Turollian *H. primigenia* (Wagner, 1848) and late Ruscinian *H. depereiti* Sen, 2001 in having the deep anteroflexid on p4. Moreover, it differs from the former by somewhat larger dimensions of p4.

**Remarks.** The age of the Kosyakino locality is believed to be early Ruscinian, MN14, based on lago-morphs (Averianov & Tesakov, 1998) or late Ruscinian, MN15, based on carnivores (Vislobokova et al., 2001). The first opinion is followed in this paper.

**Occurrence.** The type locality.

*Hystrix primigenia* (Wagner, 1848)

Figs. 3, 4.

*Lamprodon primigenius*: Wagner, 1848: 374, pl. 4, figs. 7, 8; Wagner, 1860: 129, pl. 5, fig. 13.

*Hystrix primigenia*: Gaudry & Lartet, 1856: 318; Sen & Kovatchev, 1987: 318, text-figs. 1–3; Bonis et al., 1992: 76, text-figs. 1, 2, 4, 5; Masini & Rook, 1993: 79, pl. 1, figs. 1–7; Weers, 1994: 44; Fristani et al., 1997: 158, text-fig. 2; Alcald & Montoya, 1998: 140, text-figs. 2, pl. 1, figs. 1–11.

**Hystrix bessaracica**: Riabinin, 1929: 112.

**Holotype.** Institute of Paleontology, University of Munich, ASI1146, left lower incisor incisor.

**Referred material.** Right P4 (TSPI M-2/86-1) from Mor-skaya 2 locality, the northern coast of the Taganrog Gulf of the Azov Sea. Late Miocene, late Turollian, MN13, fluvialite deposits bracketed between the marine limestone of middle Sarmatian (late Miocene) and late middle–late Pliocene Khaprovian fluvialite deposits (Bajgusheva et al., 2001).

**Type locality.** Pikermi, Greece.

**Stratigraphic level.** Late Miocene, middle Turollian, MN12.

**Description.** The large porcupine. The P4 has one large lingual root and two small labial roots. The lingual root is bent and distinctly subdivided into anterior and posterior parts by a clear groove. The anterior side of the crown is convex. The posterior wall of the crown has an attritional facet of the contact to M1. The occlusal surface of the P4 is rounded-rectangular in outline. The occlusal pattern is clearly pentalophodont. The parastyle is very distinct. There are the lingual hypoflexus and four labial synlines. The tooth is slightly worn. The hypostria starts at 10.5 mm above the base of the crown. The parafossette is nearly closed, but it still has a small parastria. The anterior and posterior mesoflexi are open, with distinct striae. The postfossette is closed. Labially to two posterior synlines, there is a large longitudinally oriented enamel island, which is a posteralabial part of the posterior mesoflexus (which can be termed lingual mesofossette).

**Measurements.** Occlusal length (L) 12.0, occlusal width (W) 9.1; crown base length (LB) 13.3, crown base width (WB) 10.8; lingual crown height (H) 15.0, labial crown height 7.7. The index of hypsodonty (H/L) 1.25. The index of robusticity (WB/LB) 0.812.

**Comparison.** *H. primigenia* differs from post-Ruscinian *Hystrix* species in larger size (Fig. 6) and less developed hypsodonty. It differs from *H. caucasia* and *H. depereiti* by smaller size. Moreover, it differs from the former in the lack of deep anteroflexid on p4. It differs from the *H. depereiti* by somewhat smaller dimensions of cheek teeth (Fig. 6) and less reduced f3 (Sen, 2001). *H. primigenia* differs from *H. gansensis* Wang & Qiu, 2002 from late Miocene of China by more divergent upper tooth rows and some cranial characters (Wang & Qiu, 2002).

**Occurrence.** Late Miocene, Turollian (MN12–13)—early Pliocene (?), Ruscinian (MN14–15) of Europe and Asia Minor.

**Discussion.**

The beaver genus *Anchitheriomys* Roger, 1898 (=*Amblycastor* Matthew, 1908) is recorded from the early-middle Miocene (MN5–6) of Europe, middle Miocene of North America and late middle Miocene of Asia (Stirton, 1934; Lytshev & Aubekeyova, 1971; Xu,
A — occlusal view, B — anterior view, C — posterior view, D — lingual view, E — labial view.

1994; Korth & Emry, 1997; Koenigswald & Mörs, 2001; Korth, 2002). This genus was referred alternatively to beavers and porcupines, and recently firmly rested within Castoridae (Koenigswald & Mörs, 2001; Korth, 2002). Argyropulo (1939) described a single tooth of a new beaver, *Amblycastor caucasicus*, from the early Pliocene of Kosyakino. Later Gromov & Baranova (1981) cited this record as *Anchitheriomys caucasicus*, also a beaver. Generic determination of this large rodent still was very doubtful or provisional (Gromov, 1962).

As showed in present study, the structure of the p4 of this form rules out its attribution to the genus

Figure 5. Length-width diagram of p4 of Hystrix species from several late Miocene — early Pliocene localities: H. caucasica (Kosyakino), H. depereti (Perpignan), Hystrix sp. (Weze), and H. primigenia (Pikermi, Monticino, and Kalimanci).

Figure 6. Length-width diagram of p4 of Hystrix species from several late Miocene — early Pliocene localities: H. depereti (Perpignan), H. trofimovi (Kuruksay), Hystrix sp. (Weze), and H. primigenia (Pikermi, Monticino, Kalimanci, Dytiko 3, Hadji Dimovo, and Morskaya 2).

Anchitheriomys (=Amblycastor) because of lack of the characteristic plication of the folds and deeper hypostrid extending to the base of the crown (Stirton, 1934; Weers, 1993; Xu, 1994; Korth & Emry, 1997). This p4 is actually a porcupine tooth.

Although beavers and porcupines are not closely related, their dentition is basically similar and isolated fossil teeth may be difficult to attribute to family. The discussed tooth possesses some superficial similarity to Castoridae because it has an anteroflexid and anterostriid, which opens on lingual crown side between the metaconid and metalophid. Commonly, Hystricidae are characterized by the connection of the mentioned elements and by closed anterofossitid. However, one very similar p4 with anterostriid is described for Hystrix primigenia from Hadji Dimovo, MN12 of Bulgaria (Sen, 1999: fig. 42.3C). Apparently, it is a primitive morphotype. H. caucasica differs from this species in having considerably larger size (Fig. 5) (Masini & Rook, 1993; Sen, 2001). The size of H. caucasica is approximately equal to H. depereti from Serrat d'en Vaquer, Perpignan, MN15 of France (Sen, 2001). The crown height of p4 of H. caucasica (H/L = 1.06) is closer to that of H. depereti (H/L = 1.11) than H. primigenia (0.86-0.92) (Sen, 2001). However, the specific 'caucasica' morphotype of p4 is not recorded in H. depereti. The holotype of the latter does not show an unambiguous anterostriid (Sen, 2001: fig. 4A). Moreover, these two species have different stratigraphic (Masini & Rook, 1993) and geographic distribution. Therefore, the taxonomic question about their conspecificity remains open. However, the species name H. caucasica is senior, and it will prevail over H. depereti if the synonymy of these species is proved.

The above described P4 of H. primigenia from Morskaya 2 is very similar in occclusal structure to upper premolars of the porcupine skull described from the late Tuorian (MN13) of Macedonia, Greece (Bonis et al., 1992). These teeth are at a slightly older wear stage thus getting a more rounded outlines (versus to elongated in the premolar from Morskaya 2) and hypofossette. They are somewhat smaller than the specimen from Morskaya 2.

The depth of hypostria correlates with evolutionary stage of hypsodonty. In Vallesian and early Tuorian Hystrix parvae hypoflexus is only about 5 mm above crown base (Weers & Montoya, 1996). In P4 of H. depereti from Perpignan (MN15) the hypostria starts at 10.7 mm above the base of the crown (Sen, 2001). On the single P4 of H. primigenia from Pikermi (MN12), the hypoflexus is already lost by wear with the calculated crown height of ca. 10.8 mm (Sen, 2001). In the old, abraded molar of H. primigenia from Las Casiones (MN13) the hypoflexus is already lost by wear at the crown height of 10.9 mm (Alcalà & Montoya, 1998). Hypoflexus of P4 in H. primigenia from Brisighella (MN13) is calculated to be ca. 13.45 mm above the crown base (Masini & Rook, 1993: pl. 2, fig. 5a). Thus, in this feature the porcupine from Morskaya 2 falls in the variability range of Tuorian and Rusciniann forms.

Last revision of the Tuorian and Rusciniann porcupines of the genus Hystrix was presented by Weers & Rook (2003). The authors reevaluated criteria of the species level taxonomy in this group. According to this viewpoint, forms with the index of hypsodonty (H/L) below 1.0 are attributed to Hystrix primigenia; values of this index between 1.0 and 1.5 define H. depereti. Thus, the Tuorian porcupines from Brisighella, Kalimanci, and Las Casiones, previously referred to H. primigenia, are transferred to H. depereti. However, the differences in values of the index of hypsodonty are clearly statistically insignificant, because most of samples contain few specimens, which belong to different wear stages. If accepted, this concept means the coexistence of two species with indistinguishable dental morphology and close size in the late Tuorian. We doubt this interpretation and for the time being adhere to the original species conception of Sen (2001), which implies the phylectic replacement of less hypsodont Tuorian H.
primigenia by more advanced Ruscinian *H. depereti*. Usage of numerical approaches as distinctive specific criteria requires statistically reliable samples.

‘*Hystrix primigenia*’ from the late Ruscinian (MN15) of Poland, Weze (Sulimski, 1960: pl. 1, figs. 1–3, pl. 2, figs. 1–5) differs from our form in slightly larger size and in the anteroloph of P4 dissected by a distinct anterolingual flexus. This perplexing feature thus far unique to the Polish form may well be an aberration. On the other hand, there is an opinion of Shevyreva (1986) of the possible generic level rank of this character. Anyway, we exclude this form from the discussion of the species *H. primigenia*.

*Hystrix trofimovi* Shevyreva, 1986 (Shevyreva, 1986; Vangengeim et al., 1988) from the late Pliocene Kuruskay locality (Tajikistan, MN17) was referred to *H. primigenia* by Weers (1994: 46). This form matches *H. primigenia* in size, general occlusal structure and low crown height. We reexamined the type material on *Hystrix trofimovi* housed in the PIN collection. We think that this form likely belongs to other lineage of porcupines, which preserved primitive appearance till late Villanyian. By that time the lineage of European porcupines was represented by much more hypsodont forms, like *H. rufossa* (Weers, 1994). *H. trofimovi* may be related to other Asian brachyodont forms, late Miocene *H. gansuensis* (Wang & Qiu, 2002) and early Pleistocene (Nihewanian) *H. zhengi* (Weers & Zhang, 1999).

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