

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

Alexey V. Lopatin, Alexey S. Tesakov & Vadim V. Titov

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. caucasica*. The species shows affinities with the group of semihypsodont 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.

Alexey V. Lopatin [alopat@paleo.ru], Paleontological Institute, Russian Academy of Sciences, ul. Profsoyuznaya 123, Moscow 117647, Russia; Alexey S. Tesakov [tesak@geo.tv-sign.ru], Geological Institute of the Russian Academy of Sciences, Pyzhevskiy per., 7, Moscow 119017, Russia; Vadim V. Titov [vvtitov@yandex.ru], Taganrog Pedagogical institute, Rosa Luxembourg str., 38, 20, Taganrog 347900, Russia.

Позднемиоценовые – раннеплиоценовые дикобразы (Rodentia, Hystricidae) юга европейской России

А.В. Лопатин, А.С. Тесаков, В.В. Титов

РЕЗЮМЕ. Ревизия систематического положения *Anchitheriomys caucasicus* (= *Amblycastor caucasicus* Argyropulo, 1939) из раннего плиоцена (ранний русциний, MN14) Северного Кавказа (Косякинский карьер), обычно относимого к бобрам (Castoridae), показала его принадлежность к дикобразам рода *Hystrix* (Hystricidae). Установлено, что его следует рассматривать как особый вид (*H. caucasica*), близкий группе семигипсодонтных дикобразов *H. primigenia* (Wagner, 1848) (MN12–13) – *H. depereti* Sen, 2001 (MN15). По размерам он крупнее *H. primigenia* и соответствует *H. depereti*. Из позднемиоценового местонахождения Морская 2 (поздний туролий, MN 13) в Приазовье описан хорошо сохранившийся P4 дикобраза, отнесенный к крупной форме *H. primigenia* (первая находка этого вида в России).

КЛЮЧЕВЫЕ СЛОВА: *Hystrix*, Hystricidae, Rodentia, поздний миоцен, ранний плиоцен, Приазовье, Северный Кавказ, Россия.

Introduction

Porcupines were common representatives of the mammal communities in the late Miocene, Pliocene, and Pleistocene of Eurasia. In last years, the knowledge of the fossil porcupines considerably increased. European forms were studied by Bonis *et al.* (1992), Weers (1993, 1994), Masini & Rook (1993), Weers & Montoya (1996), Sen (1996, 1999, 2001), Fistani *et al.* (1997), Alcalá & Montoya (1998), Weers & Rook (2003), and others. Asian records are covered by Weers (1985), Shevyreva (1986), Pei (1987), Weers & Zheng (1998), Weers & Zhang (1999), Wang & Qiu (2002). The present paper reports the first data on fossil porcupines from late Miocene and early Pliocene of south European Russia (Northern Caucasus and the Azov Sea Region).

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 caucasica (Argyropulo, 1939)
Figs. 1, 2.

Amblycastor caucasicus: Argyropulo, 1939: 638, text-figs. a–d.
Anchitheriomys caucasicus: Gromov & Baranova, 1981: 100.
Holotype. PIN 25/1, left p4.

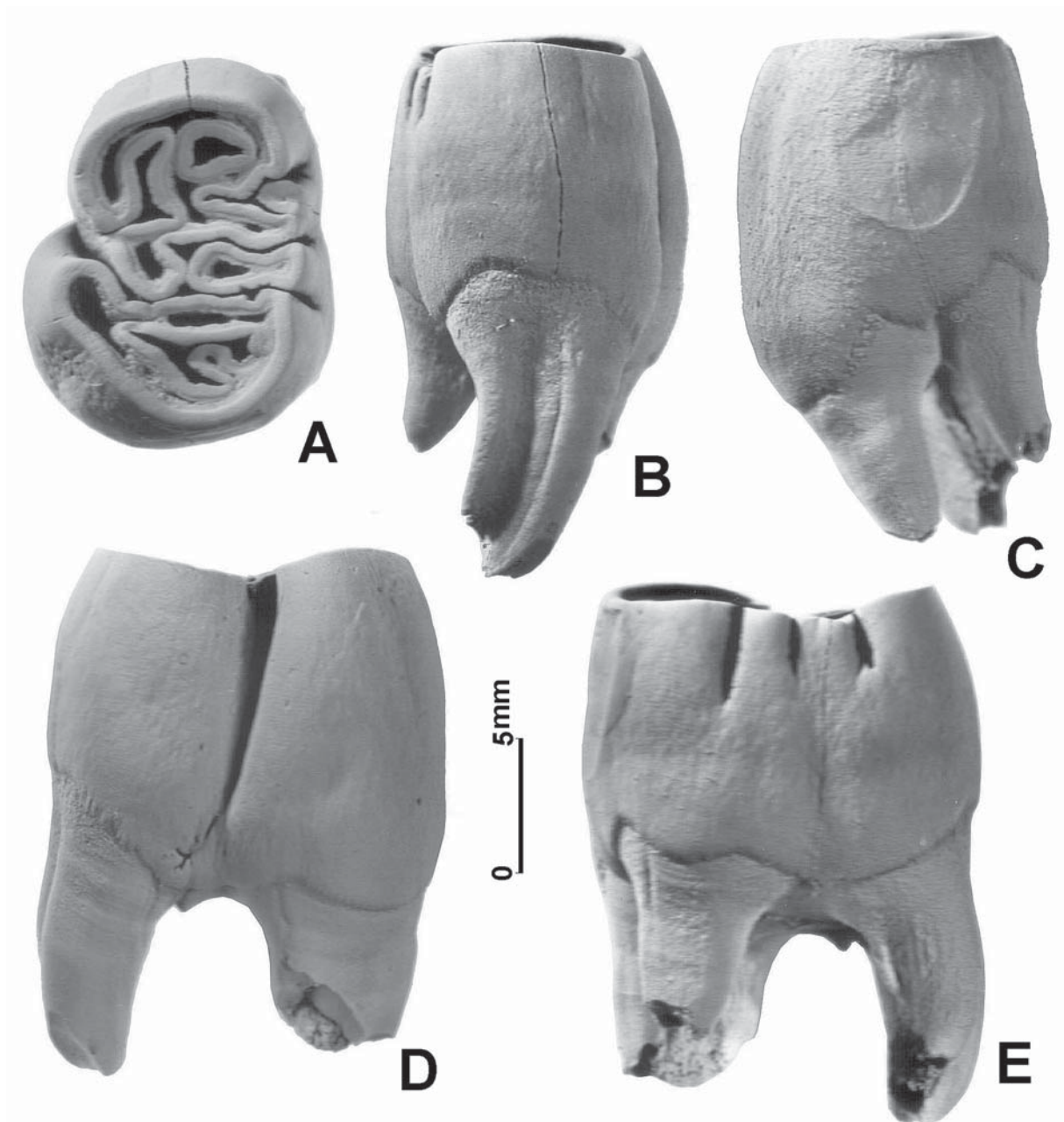


Figure 1. *Hystrix caucasica* (Argyropulo, 1939). Holotype PIN 25/1, left p4. Kosyakino sand pit, vicinity of Stavropol city, Northern Caucasus, Russia. Lower Pliocene, lower Ruscinian, MN14.

A — occlusal view, B — anterior view, C — posterior view, D — labial view, E — lingual view.

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 hypostriid 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 mesofossettid). Between the metaconid and metalophulid there is the small additional open flexid, which closely joins the anterofossettid. Therefore, this fold should be defined as an anteroflexid, and its exit groove, an anterostriid. The lingual striids run about 1/3 (posterior mesostriid) and 1/4 (anterior mesostriid and anterostriid) of the crown

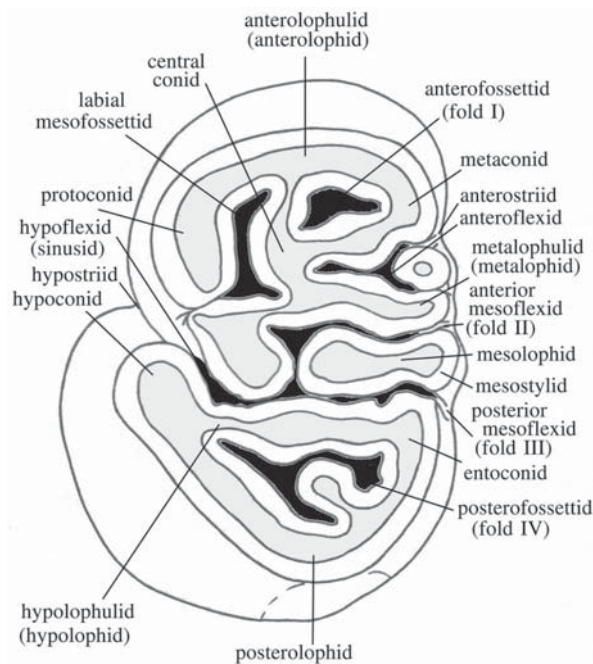


Figure 2. *Hystrix caucasica* (Argyropulo, 1939). Holotype PIN 25/1, left p4. Kosyakino sand pit, vicinity of Stavropol city, Northern Caucasus, Russia. Lower Pliocene, lower Ruscinian, MN14. The structure of the occlusal surface.

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 posterofossettid 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 posterofossettid 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. caucasica* differs from all post-Ruscinian *Hystrix* species in larger size (Fig. 5) and less developed hypsodonty. It differs from the Turolian *H. primigenia* (Wagner, 1848) and late Ruscinian *H. depereti* 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 lagomorphs (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; Fistani *et al.*, 1997: 158, text-fig. 2; Alcalá & Montoya, 1998: 140, text-figs. 2, pl. 1, figs. 1–11.

Hystrix bessarabica: Riabinin, 1929: 112.

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

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

Type locality. Pikermi, Greece.

Stratigraphic level. Late Miocene, middle Turolian, 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 synclines. The tooth is slightly worn. The hypostria starts at 10.5 mm above the base of the crown. The parafoesette is nearly closed, but it still has a small parastria. The anterior and posterior mesoflexi are open, with distinct striae. The postfoesette is closed. Labially to two posterior synclines, there is a large longitudinally oriented enamel island, which is a posterolabial 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. caucasica* and *H. depereti* by smaller size. Moreover, it differs from the former in the lack of deep anteroflexid on p4. It differs from the *H. depereti* by somewhat smaller dimensions of cheek teeth (Fig. 6) and less reduced m3 (Sen, 2001). *H. primigenia* differs from *H. gansuensis* Wang & Qiu, 2002 from late Miocene of China by more divergent upper tooth rows and some cranial characters (Wang & Qiu, 2002).

Occurrence. Late Miocene, Turolian (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 & Aubekerova, 1971; Xu,

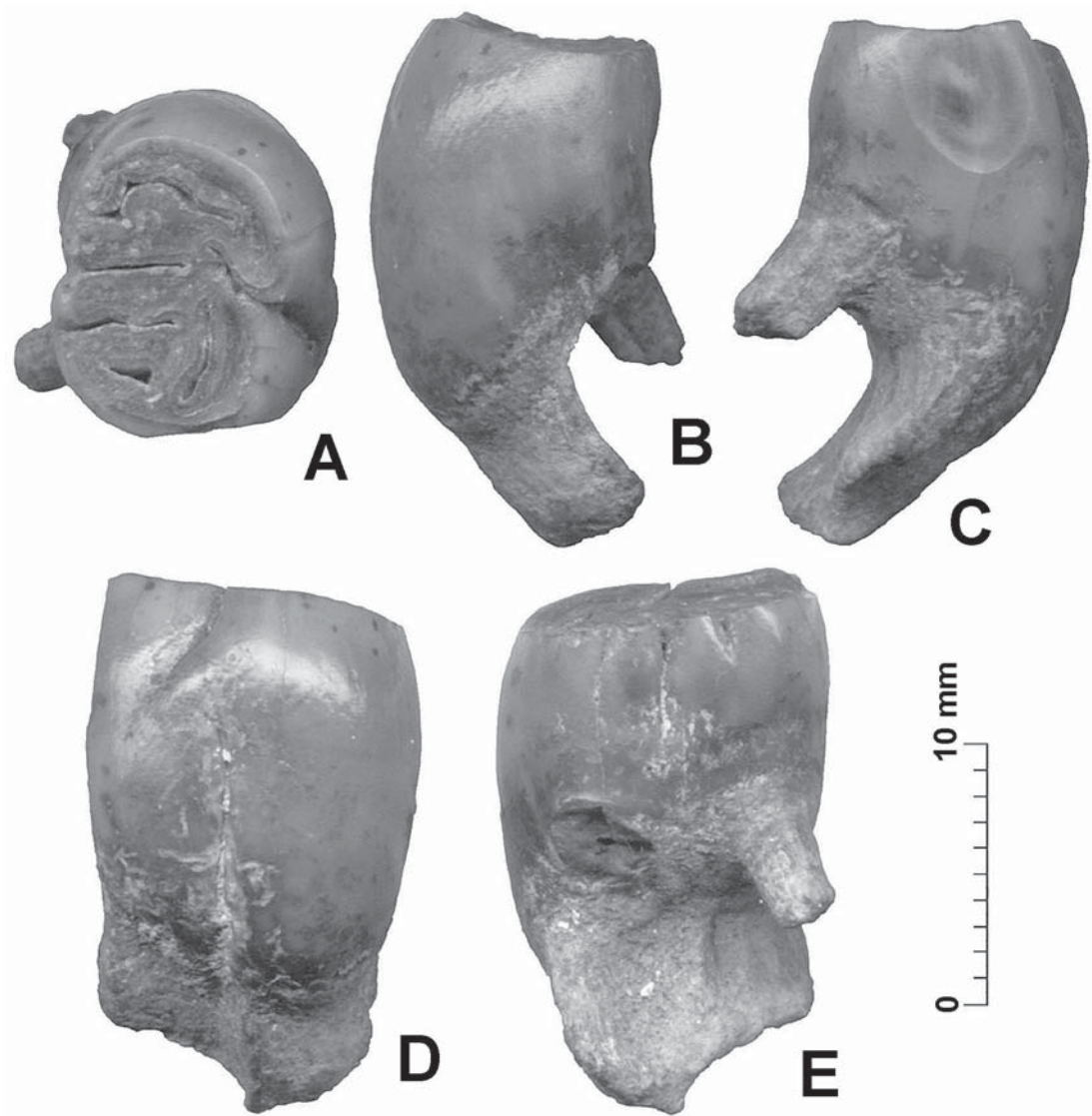
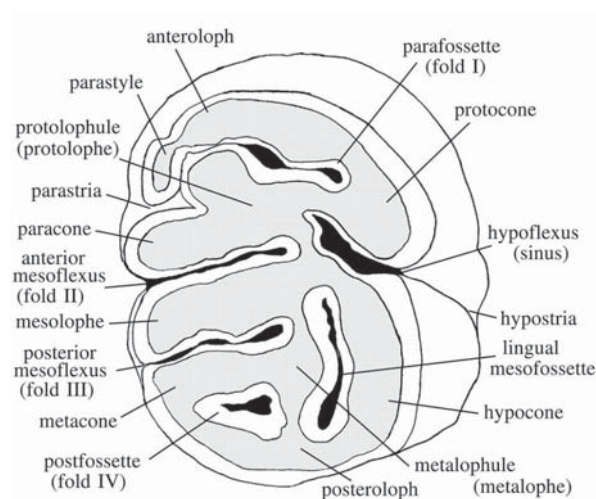


Figure 3. *Hystrix primigenia* (Wagner, 1848). TSPI M-2/86-1, right P4. Morskaya 2 locality, the northern coast of the Taganrog Gulf of the Azov Sea. Upper Miocene, upper Turolian, MN13. A — occlusal view, B — anterior view, C — posterior view, D — lingual view, E — labial view.



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 4. *Hystrix primigenia* (Wagner, 1848). TSPI M-2/86-1, right P4. Morskaya 2 locality, the northern coast of the Taganrog Gulf of the Azov Sea. Upper Miocene, upper Turolian, MN13. The structure of the occlusal surface.

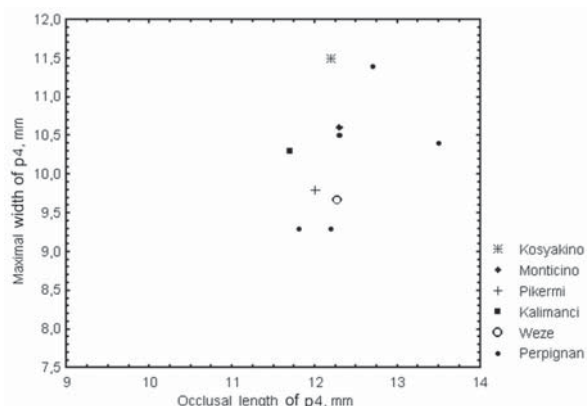


Figure 5. Length-width diagram of p4 of *Hystrix* species from several late Miocene — early Pliocene localities: *H. caucasica* (Kosyokino), *H. depereti* (Perpignan), *Hystrix* sp. (Weze), and *H. primigenia* (Pikermi, Monticino, and Kalimanci).

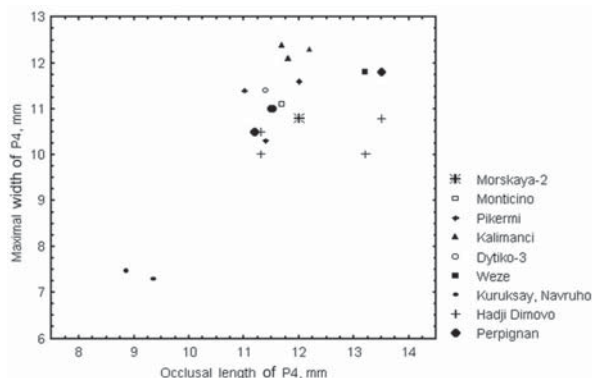


Figure 6. Length-width diagram of P4 of *Hystrix* species from several late Miocene – early Pliocene localities: *H. depereti* (Perpignan), *H. trofimovi* (Kuruksay), *Hystrix* sp. (Weze), and *H. primigenia* (Pikermi, Monticino, Kalimanci, Dytiko 3, Hadji Dimovo, and Morskaya 2).

Anchitheriomys (= *Amblycastor*) because of lack of the characteristic plication of the folds and deeper hypostriid 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 metalophulid. Commonly, Hystricidae are characterized by the connection of the mentioned elements and by closed anterofossettid. 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 occlusal structure to upper premolars of the porcupine skull described from the late Turolian (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 hypoflexus worn into hypofosette. They are somewhat smaller than the specimen from Morskaya 2.

The depth of hypostria correlates with evolutionary stage of hypsodonty. In Vallesian and early Turolian *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 (Alcalá & 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 Turolian and Ruscinian forms.

Last revision of the Turolian and Ruscinian 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 Turolian 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 Turolian. We doubt this interpretation and for the time being adhere to the original species conception of Sen (2001), which implies the phyletic replacement of less hypsodont Turolian *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 Kuruk-say 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. refossa* (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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