

## The Porcupine *Hystrix (Acanthion) vinogradovi* (Rodentia, Hystricidae) from the Early Pleistocene Taurida Locality in Crimea

Academician A. V. Lopatin<sup>a,b,\*</sup>

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**Abstract**—The remains of porcupines from the Lower Pleistocene deposits of the Taurida karstic cave discovered in 2018 in central Crimea (Zuya village, Belogorsk district) are referred to *Hystrix (Acanthion) vinogradovi* Argyropulo, 1941. This species is quite common for the Pleistocene of Eurasia. In Crimea, several isolated teeth of this species were described from the Lower Pleistocene of Tarkhankut previously.

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In 2018, during the construction of the new federal Taurida Highway, a large karstic cave was discovered in Crimea, about 15 km east of Simferopol (Zuya village, Belogorsk district), where a large quantity of Early Pleistocene vertebrate fossils were found (1.8–1.5 Ma) [1].

Among the mammal fossils were jaw fragments, isolated teeth and postcranial fragments of the small porcupine *Hystrix (Acanthion) vinogradovi* Argyropulo, 1941 [1]. This species was widely spread in the Pleistocene of Europe [2–4], but in Crimea, it has previously only been described from three isolated upper molars of a single individual from the Early Pleistocene locality on Cape Tarkhankut [3, 5].

In the structure of the skull [3] and teeth [6], *H. (Acanthion) vinogradovi* is similar to the modern Malayan porcupine *H. (Acanthion) brachyura* L., 1758, which has led some researchers to regard it as a subspecies *H. (A.) brachyura vinogradovi* [3] or to simply synonymize it with *H. (A.) brachyura* [6]. However, until paleogenetic studies are available, *H. (A.) vinogradovi*, which is known since Early Pleistocene, should retain separate species status.

Here I describe material referred to *H. (A.) vinogradovi* from the Taurida Cave housed in the Borissiak Paleontological Institute RAS (PIN) in Moscow. Terminology for tooth structures follows [7], stages (classes) of tooth wear follow [8].

Order Rodentia Bowdich, 1821

Family Hystricidae Fischer von Waldheim, 1817

Subfamily Hystricinae Fischer von Waldheim, 1817

Genus *Hystrix* Linnaeus, 1758

Subgenus *Acanthion* Cuvier, 1823

*Hystrix (Acanthion) vinogradovi* Argyropulo, 1941

*Hystrix vinogradovi*: [9, p. 90].

*Hystrix schaubi*: [10, p. 99, Fig. 6].

*Hystrix cristata minor*: [11, p. 41, Figs. 6, 7a–7c, pl. V, Figs. 1–4, pl. VI, Figs. 1–4, 6].

*Hystrix vinogradovi atavus*: [12, p. 173, pl. I, Figs. 1–9].

*Hystrix vinogradovi kudarensis*: [2, p. 47, Figs. 2, 3A, 4A, B].

*Hystrix* sp. (small form): [5, p. 21].

*Hystrix (Acanthion) brachyura vinogradovi*: [3, p. 47].

Lectotype: Zoological Institute RAS, Saint-Petersburg, ZIN 21914-0, fragment of left mandible with teeth; Azerbaijan, Binagady; Middle Pleistocene.

Description (Figs. 1–3). A small-sized porcupine with hypsodont teeth. Upper cheek teeth at different stages of tooth wear show flexi (reentrant folds) closing into fossettes (enamel islands) and then becoming decreased in size and number until they disappear completely. By analogy with *H. (A.) brachyura* [8], all tooththrows are considered belonging to juveniles that contain DP<sup>4</sup> (at any stage of tooth wear) and unworn M<sup>3</sup>; subadults are assumed to be characterized by P<sup>4</sup> at an early stage of tooth wear (stages A and B, all flexi open) and worn M<sup>3</sup>; adults are characterized by P<sup>4</sup> with distinct wear structures (stage C or later, at least one closed fossette) and worn M<sup>3</sup>; senile individuals are characterized by molars M<sup>1</sup>–M<sup>2</sup> at the most advanced stage of tooth wear (stages H2/H3, no more than one fossette, no flexi).

The maxilla of a juvenile individual, specimen PIN 5644/36 (Fig. 1) contains a heavily worn DP<sup>4</sup>

<sup>a</sup> Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, 117647 Russia

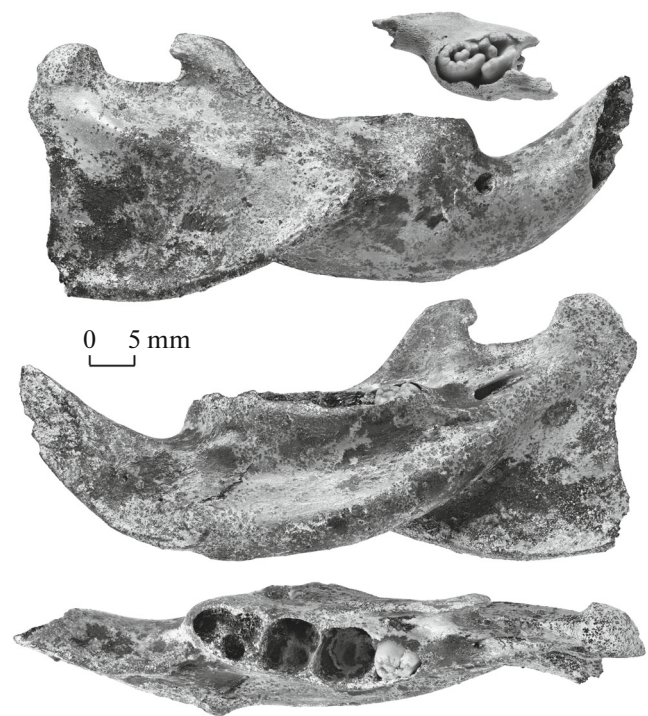
<sup>b</sup> Moscow State University, Moscow, 119992 Russia

\* e-mail: alopap@paleo.ru



**Fig. 1.** *Hystrix (Acanthion) vinogradovi* Argyropulo, 1941: specimen PIN 5644/36, fragment of right maxilla with DP<sup>4</sup> (G7), M<sup>1</sup> (E5), and M<sup>2</sup> (D1); specimen PIN 5644/39, isolated left M<sup>3</sup> (A1); specimen PIN 5644/41, fragment of left maxilla with DP<sup>4</sup> (G8), M<sup>1</sup> (F4), M<sup>2</sup> (D5) and M<sup>3</sup> (A1); specimen PIN 5644/40, isolated right P<sup>4</sup> (A1); specimen PIN 5644/37, fragment of left maxilla with P<sup>4</sup> (F4) and M<sup>1</sup> (G7); specimen PIN 5644/38, fragment of right maxilla with P<sup>4</sup> (G4), M<sup>1</sup> (G8), and M<sup>2</sup> (G7) (from top to bottom); Crimea, Taurida Cave; Lower Pleistocene.

(stage G7), moderately worn M<sup>1</sup> (stage E5), and slightly worn M<sup>2</sup> (stage D1). DP<sup>4</sup> is without flexi, with five small fossettes (hypofossette, parafossette, anterior, posterior and lingual mesofossettes) and a tiny enamel island in place of the postfossette. M<sup>1</sup> has completely formed parafossette and postfossette; anterior and posterior mesoflexi are closed labially, dentine fields of surrounding lophs are merged; the anterior mesofossette connects with the hypoflexus, the posterior mesofossette confluent with the lingual mesofossette. M<sup>2</sup> has a parafossette isolated from the hypoflexus and closed labially, but the dentine fields of the anteroloph and the protoloph are separate; the anterior mesoflexus is connected with the hypoflexus, posterior mesoflexus open labially, lingual mesoflexus



**Fig. 2.** *Hystrix (Acanthion) vinogradovi* Argyropulo, 1941: specimen PIN 5644/42, fragment of left mandible with P<sub>4</sub> at the eruption stage, occlusal view; specimen PIN 5644/35, fragment of right mandible with M<sub>3</sub> at the eruption stage and the alveoli of the incisor and DP<sub>4</sub>–M<sub>2</sub> in labial, lingual and occlusal view (from top to bottom); Crimea, Taurida Cave; Lower Pleistocene.

open distally, dentine fields of the hypocone and posteroloph separate; the posterior and the lingual mesoflexi are connected but not fully confluent; postfossette closed, but the dentine fields of the metaloph and the posteroloph remain separate labially.

The upper jaw of a juvenile individual, specimen PIN 5644/41 shows more advanced wear on teeth: very heavily worn DP<sup>4</sup> (stage G8), heavily worn M<sup>1</sup> (stage F4) and moderately worn M<sup>2</sup> (stage D5). DP<sup>4</sup> has four small fossettes: hypofossette, parafossette, anterior mesofossette and a merged fossette in place of the posterior and the lingual mesofossettes. M<sup>1</sup> has a hypoflexus and four fossettes, with the parafossette and the postfossettes being very small. The anterior mesofossette approaches the end of the hypoflexus, the posterior mesofossette merged with the lingual mesofossette into a single long fossette. M<sup>2</sup> has the anterior and the posterior mesoflexi open labially, the anterior mesoflexus separated from the hypoflexus, the parafossette isolated, the postfossette small, all dentine fields merged. M<sup>3</sup> at the stage of eruption, completely unworn (stage A1), with open flexi and a very short hypostria.

Also belonging to a juvenile individual is an isolated M<sup>3</sup> (specimen PIN 5644/39) at an initial stage of wear

(A1). Its occlusal surface is formed by enamel cusps and ridges, with all the flexi open (paraflexus, anterior mesoflexus, posterior mesoflexus, postflexus (labial folds I, II, III, and IV, respectively), and hypoflexus), the hypostria is long.

The occlusal surface of an unworn (stage A1) P<sup>4</sup> (specimen PIN 5644/40) is formed by enamel-covered large cusps and ridges, all flexi open, the anterior mesoflexus joined in the middle with the lingual mesoflexus. The lingual enamel crown height almost twice the length of the occlusal surface. The height of the hypostria is about 40% of the lingual enamel crown height, labial folds distinct, the deepest folds II and III up to two-fifths of the hypostria height.

The maxilla of an adult individual, specimen PIN 5644/37 contains a fairly heavily worn P<sup>4</sup> (stage F4) and a very heavily worn M<sup>1</sup> (stage G7). P<sup>4</sup> has a deep hypoflexus and four fossettes. The parafossette and the anterior mesofossette are relatively long, transversely elongated. The other fossettes (the lingual mesofossette and the single fossette in place of the posterior mesofossette and the postfossette) are oriented sublongitudinally. M<sup>1</sup> has five closed fossettes (parafossette, anterior, posterior, and lingual mesofossettes and hypofossette).

The maxilla of an adult individual, specimen PIN 5644/38 contains a very heavily worn P<sup>4</sup> (stage G4), M<sup>1</sup> (stage G8), and M<sup>2</sup> (stage G7). P<sup>4</sup> has seven fossettes: the parafossette, anterior mesofossette, posterior mesofossette (merged with the lingual mesofossette), two enamel islands in place of the hypofossette and two enamel islands in place of the postfossette. M<sup>1</sup> has four clearly distinct fossettes (the anterior, the posterior, and lingual mesofossettes and hypofossette) and a tiny enamel island in place of the parafossette. M<sup>2</sup> has five distinct fossettes: the parafossette, the anterior, the posterior, and the lingual mesofossettes, and the hypofossette.

The mandible of a juvenile individual with an incompletely erupted M<sub>3</sub> (specimen PIN 5644/35) fairly deep and massive, the coronoid and the articular processes almost equal in height (Fig. 2). The angular process is extensive, extending ventrally to the level of the lower edge of the corpus mandibulae, distally its apex in line with the articular condyle. The mental foramen located below the posterior ending of the diastema. The lower masseter ridge high, beginning below the anterior part of the alveolus of M<sub>1</sub>. The symphysis reaches the level of the middle of the alveolus of the premolar (DP<sub>4</sub>/P<sub>4</sub>). The alveolar buldge of the lower incisor greatly inflated.

P<sub>4</sub> at the eruption stage (O1) has an occlusal surface that is elongated longitudinally and shows the structure that is typical for the species [2]: it consists of two enamel cusps (the central conid and the eminence of the hypolophid), surrounded by a high ridge, shallowly incised by grooves and folds, which includes the



Fig. 3. *Hystrix (Acanthion) vinogradovi* Argyropulo, 1941, specimen PIN 5644/44, broken right humerus; Crimea, Taurida Cave; Lower Pleistocene.

protoconid, the anterolophid, the metaconid, the mesostylid, the entoconid, the posterolophid and the hypoconid (specimen PIN 5644/42). All the folds are open, the posterior mesoflexid and the posteroflexid have distinctly narrow openings, whereas the exits of the anterior mesoflexid, the anterofossettoid and the labial mesofossettoid are marked by superficial grooves. The hypoflexid is extensive, the hypostriid is very deep.

The tooth crown of M<sub>3</sub> at the eruption stage (O1), consisting of fully enamel-covered cusps and ridges, rises above the labial wall of the alveolus, but the lingual margin of the occlusal surface is located below the lingual wall of the alveolus (specimen PIN 5644/35).

Measurements in mm. Upper incisors (longitudinal diameter × transverse diameter), 8.0 × 5.5 (specimen PIN 5644/34); 9.0 × 5.8 (specimen PIN 5644/45).

Specimen PIN 5644/36, upper cheek teeth (length × width): DP<sup>4</sup> (G7), 7.2 × 7.0; M<sup>1</sup> (E5) 7.3 × 7.0; M<sup>2</sup> (D1), 7.5 × 6.0; lingual enamel crown height of M<sup>2</sup>, 16.5.

Specimen PIN 5644/41, upper cheek teeth (length × width): DP<sup>4</sup> (G8), 6.0 × 5.5; M<sup>1</sup> (F4), 6.6 × 6.9; M<sup>2</sup> (D5), 7.1 × 5.5; M<sup>3</sup> (A1), 5.7 × 4.5; length of tooththrow DP<sup>4</sup>–M<sup>3</sup>, 25.5.

Specimen PIN 5644/37, P<sup>4</sup> (length × width), 8.1 × 6.9 (F4).

Specimen PIN 5644/38, upper cheek teeth (length  $\times$  width): P<sup>4</sup> (G4), 7.0  $\times$  6.8; M<sup>1</sup> (G8), 5.6  $\times$  6.7; M<sup>2</sup> (G7), 6.5  $\times$  7.0.

Specimen PIN 5644/40, P<sup>4</sup> (A1): length of occlusal surface, 8.7; maximum crown length, 9.5; width of occlusal surface, 6.5; maximum crown width, 7.5; lingual enamel crown height, 17.2; hypostria height, 6.5; height of labial folds: I, 0.8, II, 2.5, III, 2.5, IV, 1.5.

Specimen PIN 5644/39, M<sup>3</sup> (A1): length of occlusal surface, 6.0; maximum crown length, 6.3; width of occlusal surface, 4.0; maximum crown width, 5.7; lingual enamel crown height, 12.2; hypostria height, 4.0; height of labial folds: I, 1.5, II, 0.8, III, 1.0, IV, 0.2.

Specimen PIN 5644/42, P<sub>4</sub> (O1): length of occlusal surface, 8.6.

Specimen PIN 5644/35, mandible: length, 70.0; height at the coronoid process, 30.0; depth below M<sub>1</sub> lingually, 18.0; length of the cheek teeth row along the alveoli, 27.0; alveoli (length  $\times$  width): DP<sub>4</sub>, 8.0  $\times$  5.6; M<sub>1</sub>, 6.0  $\times$  6.5; M<sub>2</sub>, 6.5  $\times$  6.8; occlusal surface (length  $\times$  width) M<sub>3</sub> (O1), 5.5  $\times$  4.8.

Specimen PIN 5644/43, alveoli (length  $\times$  width): M<sub>1</sub>, 7.0  $\times$  7.5; M<sub>2</sub>, 7.0  $\times$  7.5; M<sub>3</sub>, 7.5  $\times$  6.5.

Humerus (specimen PIN 5644/44, Fig. 3): maximum width of the distal end of the humerus, 31.0; minimum width of the diaphysis, 10.0.

Comparison and remarks. The structure and size of the teeth and the mandible from the Taurida Cave corresponds to *H. (A.) vinogradovi* and differs from other species of the genus. The coronoid process of the mandible is noticeably more developed than in the modern species *H. (A.) brachyura*.

*H. (A.) vinogradovi* differs clearly from the other Pleistocene members of the genus by the combination of small size and hypsodont cheek teeth. The other Pleistocene hypsodont species is *H. (H.) refossa* Gervais, 1852, sometimes found together with *H. (A.) vinogradovi* [12], but much larger in size [13, 14]. According to D. van Weers [6, 14], the synonyms of *H. (H.) refossa* are *H. major* Gervais, 1859, *H. etrusca* Bosco, 1898 (Europe), *H. angressi* Frenkel, 1970 (Israel), *H. makapensis* Greenwood, 1958 (South Africa), *H. crassidens* Lydekker, 1886 (India), *H. gigantea* Van Weers, 1985 (Java, Indonesia), and *H. magna* Pei, 1987 (China).

The length of DP<sub>4</sub>–M<sub>3</sub> (27 mm) in the Crimean form falls with the range for *H. (A.) vinogradovi* (24.0–30.4 mm), while the length of DP<sub>4</sub>–M<sup>3</sup> (25.5 mm) is even below the lower limit known for this species (28.4–30.7 mm); *H. (H.) refossa* has much higher limits (P<sub>4</sub>–M<sub>3</sub>, 39.8–43.5 mm; P<sup>4</sup>–M<sup>3</sup>, 37.5–39.7 mm) [13]. The lengths of individual worn upper cheek teeth (P<sup>4</sup>, 7.0–8.1 mm, M<sup>1–2</sup>, 5.6–7.5 mm) also correspond to *H. (A.) vinogradovi* (P<sup>4</sup>, 5.6–8.5 mm, M<sup>1–2</sup>, 5.8–8.2 mm) and are generally much smaller than in *H. (H.) refossa* (P<sup>4</sup>, 8.7–11.6 mm, M<sup>1–2</sup>, 6.8–10.6 mm)

[13, 14]. The length of the occlusal surface of P<sup>4</sup> (8.7 mm) and P<sub>4</sub> (8.6 mm) at the eruption stage in the porcupine from the Taurida Cave falls above the range known for *H. (A.) vinogradovi* (P<sup>4</sup>, 8.5, P<sub>4</sub>, 8.0); however, P<sub>4</sub> of *H. (H.) refossa* is much larger still (9.6–13.0 mm), and the minimum length of P<sup>4</sup> (8.7 mm) is observed in a single specimen, whereas for the other finds this value exceeds 9 mm and are usually more than 10 mm [13, 14]. In the degree of hypsodonty (the ratio of the enamel crown height to the length of the occlusal surface), the Crimean form (unworn P<sup>4</sup>, 1.98, worn M<sup>2</sup>, 2.2, unworn M<sup>3</sup>, 2.03) generally corresponds to *H. (A.) vinogradovi*, while falling below *H. (H.) refossa* (up to 2.6) [14] in maximum values. Considering that the variability of tooth size in *H. (A.) vinogradovi* is still incompletely known [14], the entire material from the Taurida Cave is referred to this species.

According to D. van Weers [14], the synonyms for *H. (A.) vinogradovi* are *H. schaubi* Brunner, 1954 (Late Pleistocene of Bavaria, Germany), *H. cristata minor* Malez, 1963 (Late Pleistocene of Croatia), *H. vinogradovi atavus* Janossy, 1972 (Early Pleistocene of Hungary) and *H. vinogradovi kudarensis* Baryshnikov et Baranova, 1982 (Late Pleistocene of Georgia). The range of the species at different stages of its history has likely been disjunct, which must have led to the separation of some geographic forms. *H. (A.) vinogradovi* population existed in Late Pleistocene in Western, Central, Southern, and Southeastern Europe, in Crimea, Transcaucasia (notably, the subspecific status of *H. vinogradovi kudarensis* is morphologically well founded, see [2]), the Urals and the Altai Mts. [3, 4]. Until further material becomes available, the question of whether subspecies status should be accorded to the Crimean form must remain open.

The modern Malayan porcupine *H. (A.) brachyura* inhabits the woodlands and open areas close to forests in Southern and Southeastern Asia. *H. (A.) vinogradovi*, which is likely close to this species, occurred in similar environments in the subtropical to moderately mild climate.

Occurrence. Pleistocene of Eurasia (according to A. Vekua et al. [15], the species may have existed until the Middle Holocene in western Georgia).

Material. From the Taurida Cave, fragments of maxillae with DP<sub>4</sub>–M<sup>3</sup> (specimen PIN 5644/41), with DP<sub>4</sub>–M<sup>2</sup> (specimen PIN 5644/36), with P<sup>4</sup>–M<sup>1</sup> (specimen PIN 5644/37), with P<sup>4</sup>–M<sup>2</sup> (specimen PIN 5644/38), isolated fragmentary upper incisors (specimen PIN 5644/34, 45, 46), P<sup>4</sup> (specimen PIN 5644/40), M<sup>3</sup> (specimen PIN 5644/39); mandible with M<sub>3</sub> at the eruption stage and alveoli for the incisor and for DP<sub>4</sub>–M<sub>2</sub> (specimen PIN 5644/35), fragments of mandibles with P<sub>4</sub> at the eruption stage (specimen PIN 5644/42), with alveoli of cheek teeth (specimen PIN 5644/43), fragment of a humerus with the distal epiphysis (specimen PIN 5644/44).

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## COMPLIANCE WITH ETHICAL STANDARDS

The author declares that he has no conflict of interest. This article does not contain any studies involving animals or human participants performed by the author.

## REFERENCES

1. Lopatin, A.V., Vislobokova, I.A., Lavrov, A.V., et al., *Dokl. Biol. Sci.*, 2019, vol. 485, no. 3, pp. 381–385.
2. Baryshnikov, G.F. and Baranova, G.I., *Tr. Zool. Inst. Akad. Nauk SSSR*, 1982, vol. 115, pp. 46–53.
3. Baryshnikov, G.F., *Russ. J. Theriol.*, 2003, vol. 2, no. 1, pp. 43–47.
4. Kuzmin, Y.V., Kosintsev, P.A., Vasiliev, S.K., Fadeeva, T.V., and Hodgins, G.W.L., *Quatern. Sci. Rev.*, 2017, vol. 161, pp. 117–122.
5. Topachevskii, V.A., *Gryzuny tamanskogo faunisticheskogo kompleksa Kryma* (Rodents of the Taman Faunistic Complex of the Crimea), Kiiiv: Naukova Dumka, 1973.
6. van Weers, D.J., *Contrib. Zool.*, 2005, vol. 74, nos. 3–4, pp. 301–312.
7. Lopatin, A.V., Tesakov, A.S., and Titov, V.V., *Russ. J. Theriol.*, 2003, vol. 2, no. 1, pp. 26–32.
8. van Weers, D.J., *Bijdrag. Dierkunde*, 1990, vol. 60, no. 2, pp. 121–134.
9. Argiropulo, A.I., *Priroda*, 1941, no. 3, pp. 88–91.
10. Brunner, G., *Neues Jahrbuch Geol. Paläontol. Abh.*, 1954, vol. 100, pp. 83–118.
11. Malez, M., *Paleontol. Jugosl.*, 1963, vol. 5, pp. 1–193.
12. Jánossy, D., *Vertebr. Hung.*, 1972, vol. 13, pp. 163–182.
13. Salari, L. and Sardella, R., *Mem. Atti Soc. Tosc. Sci. Nat. Ser. A*, 2011, vol. 116, pp. 171–178.
14. van Weers, D.J., *Scripta Geol.*, 1994, vol. 106, pp. 35–52.
15. Vekua, A., Bendukidze, O., Bukhsianidze, M., et al., *Bull. Georg. Nat. Acad. Sci.*, 2010, vol. 4, no. 3, pp. 140–149.

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