

A skull of *Hystrix primigenia* from the late Miocene of Macedonia (Greece)

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With 5 figures and 3 tables in the text

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Abstract: A hystricid skull from the late Turolian (MN 13) of the lower Axios valley (Macedonia, Greece) is studied. It is described, compared with other samples from the Neogene of Europe and it is determined to *Hystrix primigenia*. The stratigraphic range of the genus in Europe is also discussed.

Zusammenfassung: Ein *Hystrix*-Schädel aus dem jüngeren Turolium (MN 13) wird beschrieben, mit anderen neogenen Funden aus Europa verglichen und in stratigraphischen Zusammenhängen betrachtet.

Introduction

The late Miocene mammalian localities of the lower Axios valley (Macedonia, Greece), discovered during the last two decades, have yielded abundant material. Among the fossils recovered the hystricids were few and they have been found only in the locality "Dytiko 3", DKO. This locality belongs to Dytiko Formation and it has been dated to late Turolian, MN 13 (BONIS et al. 1988). The hystricids had not been reported previously from the Neogene of Macedonia, where they are only known from Villafranchian (KOLIADIMOU & KOUFOS 1991). However the family was found in southern Greece and in the neighbouring countries. Remains of *Hystrix primigenia* have been reported from Pikermi, Samos, Halmyropotamos (Evia) and Alifakas (Thessaly), (GAUDRY 1862–1867; SOLOUNIAS 1981; MELENTIS 1967; MELENTIS & SCHNEIDER 1966). The same species is also reported from Sandanski basin (Bulgaria), Umen Dol (Yugoslavia), Weze (Poland), Rousillon (France), Villaroya and Layna (Spain), (SEN & KOVATCHEV 1987; GAREVSKI 1956; SULIMSKI 1960; DÉPÉRET 1890; AGUSTI et al. 1987). A new species named *Hystrix bessarabica* was described from Taraklia (USSR) by RIABININ (1929), which later was transferred

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to *Hystrix primigenia* (SULIMSKI 1960). In Turkey neogene porcupines, referred as *Hystrix* sp., are known from the Turolian localities of Çoban Pinar and Bayirköy (OZANSOY 1965; UNAY & BRUIJN 1984). According to SEN & KOVATCHEV (1987) this material is similar to *H. primigenia*. The Plio-Pleistocene hystricids of Europe have been described under various specific names. *Hystrix refossa* is known from Perrier and St-Vallier in France (GERVAIS 1848–1852; VIRET 1854). Another species, *H. major* is known from Ratoneau and Montsaunès (France), Venta Micena (Spain), and Gerakarou (Macedonia, Greece), (GERVAIS 1859; HARLÉ 1910; AGUSTI et al. 1987; KOLIADIMOU & KOUFOS 1991). The species *Hystrix etrusca* has been reported from the Villafranchian of Italy (BOSCO 1898). Some other species are known as *Hystrix vinogradovi* from Hungary (MOTTL 1967) and *Hystrix suevica* from Germany (SULIMSKI 1960).

In this article the new material from the Neogene of Macedonia will be described and compared with the known material from various European localities. The studied skull is stored in the Museum of the Laboratory of Geology and Palaeontology, University of Thessaloniki, Greece.

Palaeontology

Order: Rodentia BOWDICH, 1821

Family: Hystricidae BURNETT, 1830

Genus: *Hystrix* LINNÉ, 1758

Hystrix primigenia (WAGNER, 1848)

Locality: "Dytiko 3", DKO, Macedonia, Greece.

Age: Late Turolian, MN 13, (late Miocene).

Material: Skull, DKO-41.

Description

The studied skull, DKO-41, is badly preserved except the maxilla with both toothrows, the premaxillae with the incisors and the posterior part of the skull. The dimensions of the skull and the teeth (Tab. 1, 3) indicate that we are dealing with a large porcupine. The premaxillae are narrow and curved, giving the alveoles for the incisors. In their anterior-ventral part there is a crest across to the line connected the premaxillar bones. In the left side of the skull occurs the beginning of a small jugal arch above the anterior border of P4/, which turns towards the front and labial side. The orbits and the nasal region were destroyed; however some parts of the nasals are preserved on the right side of the skull. The nasal opening is short and its posterior border is situated above the middle of the diastema I1/-P4/. The braincase is enlarged at the level of the orbits but behind the glenoid fossae it is narrow and cylindrical-shaped. There is a strong sagittal crest. The auditory bullae are large, oval and their anterior borders are

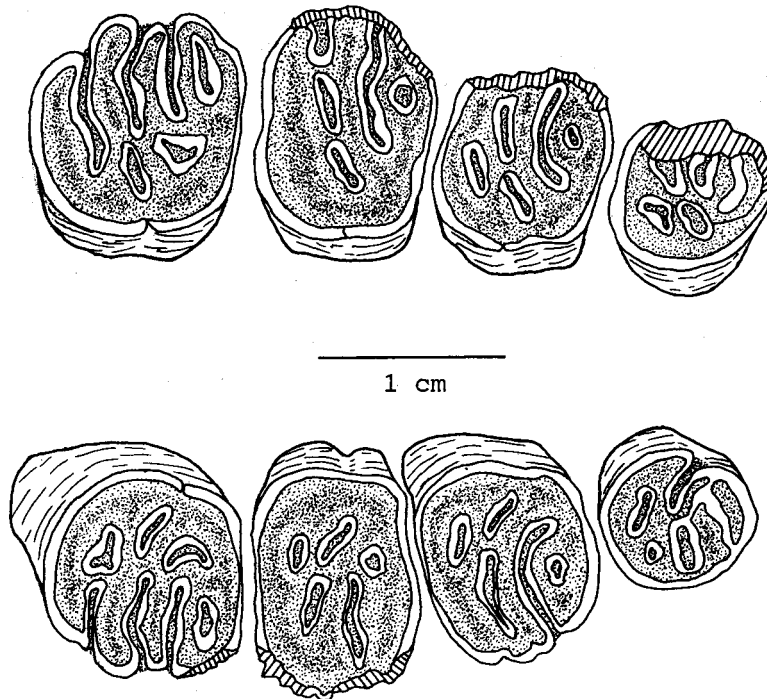


Fig. 1. *Hystrix primigenia*, "Dytiko 3", DKO, Macedonia, Greece. Upper dentition of the skull DKO-41.

Table 1. *Hystrix primigenia*, "Dytiko 3", DKO, Macedonia, Greece. Cranial measurements.

1. Length prosthion-occipital	188.0
2. Basilar length	162.0
3. Length occipital-posterior border of the nasal cavity	151.0
4. Length of nasals (from the alveoles of I1/to the end of the nasal cavity)	57.0
5. Length alveole of I1/to the anterior border of choanae	94.5
6. Length of the diastema I1/-P4/	62.0
7. Length basion-anterior border of choanae	68.0
8. Length P4/ - anterior border of choanae	33.0
9. Breadth at the base of zygomatic arcs	62.0
10. Palatal breadth between P4/	11.5
11. Idem between M3/	8.5
12. Max. breadth of the occipital condyles	31.5
13. Height from the alveole of M3/to the frontals	70.0
14. Occipital height	52.5
15. Length P4/-M3/	40.0

well behind the glenoid fossae. The palate is narrow and relatively long. Its breadth decreases from P4/ to M3/; the palatal breadth between the middle of P4/ is 11.5 mm and of M3/ 8.5 mm. The choanae are elongated, triangular-shaped and their anterior border is situated at the middle of M3/.

The dentition of the skull DKO-41 is complete and well preserved except the left molars, which are broken in their labial margin (Fig. 1). The incisors are stout and strongly curved with well developed enamel in their anterior wall, which is extended as far as the middle of the external wall and to $\frac{1}{3}$ of the internal wall. The cross section is oval-triangular with the enamel side semicircular-shaped. The enamel in the anterior wall of the incisors has a yellow and grey pigmentation. This kind of pigmentation is also referred for the incisors of *H. primigenia* from Pikermi and Weze (GAUDRY 1862–1867; SULIMSKI 1960). The dimensions of the incisors are given in Tab. 2.

Table 2. Measurements of the upper incisors of *Hystrix primigenia* from various localities.

	Dytiko DKO-41		Pikermi PMNH PIK 3191	Weze SULIMSKI (1960)
	dex	sin	sin	dex
L	6.2	6.5	6.1	6.5
1	8.3	8.7	8.0	8.5

The cheek teeth size decreases from P4/ to M3/ (Fig. 1); the teeth are very worn especially M1/. For the nomenclature of the teeth morphology see AGUSTI et al. (1987). P/4 with quadrangular shape has a rounded mesiolingual border. Both syncline I and III have been separated into two islets; the external islets are open labially. The syncline II is also open lingually while the syncline IV forms a small islet in the disto-labial corner of the tooth. The sinus is also separated as an islet (Fig. 1). M1/ is rectangular-shaped and the advanced attrition has separated all the enamel loops as isolated islets. M2/ has a rectangular shape but the distal border is smaller than the mesial one. The synclines I, II and IV and the sinus have been separated as enamel islets, but the syncline III is still open labially (Fig. 1). M3/ is smaller and less worn than the other molars and has a more or less rounded shape. This is due to the decrease of its breadth from the mesial to the distal part of the tooth and to the rounded distal margin. This roundness of M3/ is a character which is clear in Pikermi, Kalimanci and Weze (Fig. 2). The sinus is open lingually. The syncline I has been separated into two islets; the synclines II, III and IV are isolated and less worn.

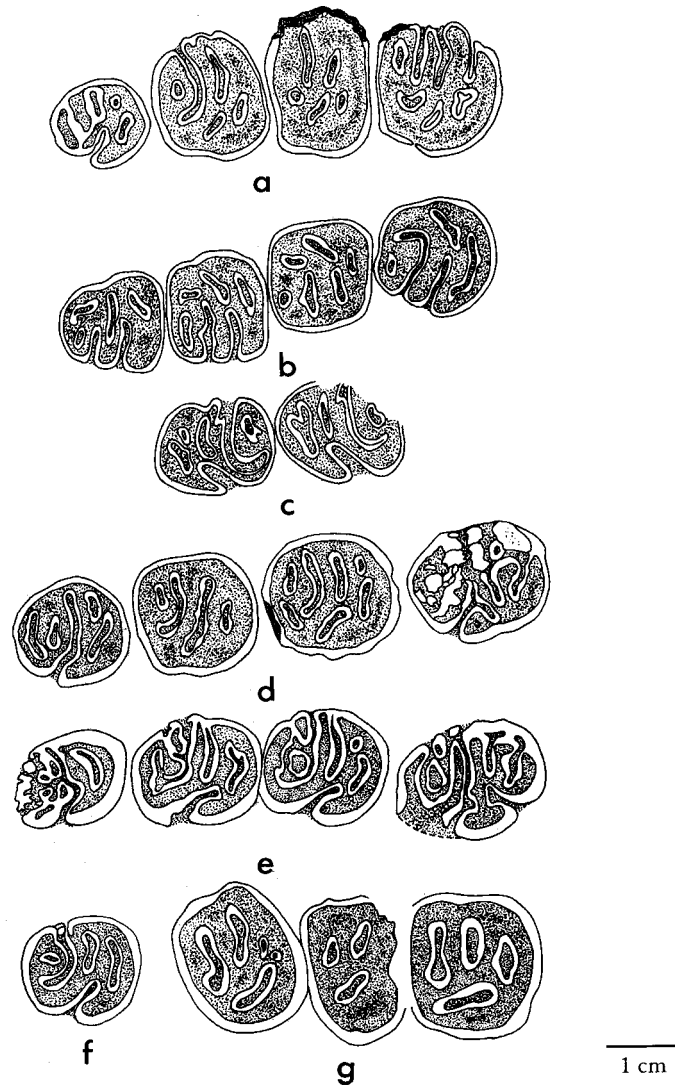


Fig. 2. *Hystrix primigenia*, upper tooththrows from various localities. — a. P4/-M3/ sin, DKO-41. b. P4/-M3/ dex, Pikermi (Greece), PMNH PIK-3116, redrawn from GAUDRY (1862–67, pl. 28, fig. 3). c. M1/-M2/ sin, Alifakas (Thessaly, Greece), Ath. No 1966/35; redrawn from MELENTIS & SCHNEIDER (1966, fig. 4). d. P4/-M3/ dex composed of isolated teeth, Kalimanci (Bulgaria); redrawn from SEN & KOVATCHEV (1987, fig. 1c). e. P4/-M3/ dex, Weze (Poland); redrawn from SULIMSKI (1960, pl. I, fig. 3). f. M2/ dex, Layna (Spain); redrawn from AGUSTI et al. (1987, fig. 6). g. P4/-M2/, Villaroya (Spain); redrawn from AGUSTI et al. (1987, fig. 6).

Discussion

The type locality of *Hystrix primigenia* is Pikermi from where a lot of material is known. The species was erected on a lower incisor under the name *Lamprodon primigenius* (WAGNER 1848). Some years later two isolated teeth from Pikermi were described as *Castor atticus* (ROTH & WAGNER 1854). The name *Hystrix primigenia* was given by GAUDRY & LARTET (1856) for a mandible with the morphological characters of both above mentioned specimens and later for some cranial remains (GAUDRY 1862–1867). Recently in a new locality (Chomateri) near Pikermi some material of *H. primigenia* was found but no description until now (BACHMAYER et al. 1982). Two cranial parts with the dentition from Pikermi were mentioned by GAUDRY (1862–1867) but we found only one maxilla in the Paris Museum (MNHN PIK 3116). The description of the material is poor and no illustrations were given except of the above mentioned maxilla (Fig. 2b). The morphology of the teeth, and their shape, especially of P4/ and M3/ are similar to those of DKO-41. There is only a difference in the number of the enamel islets and loops but this is due to the different stage of wear. However the number of the enamel islets and loops is 5–6, while in DKO-41 ranges from 5–7. Moreover the absolute dental dimensions and the robusticity indices of the teeth are similar to those of DKO-41 (Tab. 3, Fig. 3). A left series of M1/-M2/ were described from the area of the village Alifakas (Thessaly) by (MELENTIS & SCHNEIDER 1966). The sinus is still open lingually and the syncline III is open labially (Fig. 2c). The number of the loops and islets is 5–6. The open sinus and the slightly smaller dimensions (Fig. 3) of the Alifakas teeth are not significant differences from DKO-41 because they are due to the less attrition of Alifakas teeth. The species *Hystrix primigenia* appears also in the faunistic list of Samos (SOLOUNIAS 1981) but we could not find any description of this material in the bibliography.

A nice collection, consisting of upper and lower cheek teeth and mandibular pieces of *H. primigenia* has been described from Bulgaria. The material comes from Kalimanci level IV and includes one palate with P4/-M3/ dex and P4/-M1/ sin, a left maxillary piece with M1/-M3/ sin, mandibular fragments and some isolated teeth (SEN & KOVATCHEV 1987, fig. 1). The shape and the enamel morphology of the DKO-41 teeth are similar to those of Kalimanci, especially the occlusal shape of M3/ (Fig. 2d). The number of the enamel loops and islets ranges from 4–7 in Kalimanci material versus 5–7 in DKO-41. The dental dimensions and the proportions of DKO teeth are close to those from Kalimanci (Tab. 3, Fig. 3).

A good sample of *Hystrix primigenia* was described from Weze (Poland) by SULIMSKI (1960), who considered this similar to the Pikermi sample except some differences in the occlusal enamel pattern of the teeth. The teeth of DKO-41 are similar in morphology and dimensions with those from Weze (Fig. 2e, 3; Tab. 3), except of some differences in the enamel pattern, which are due

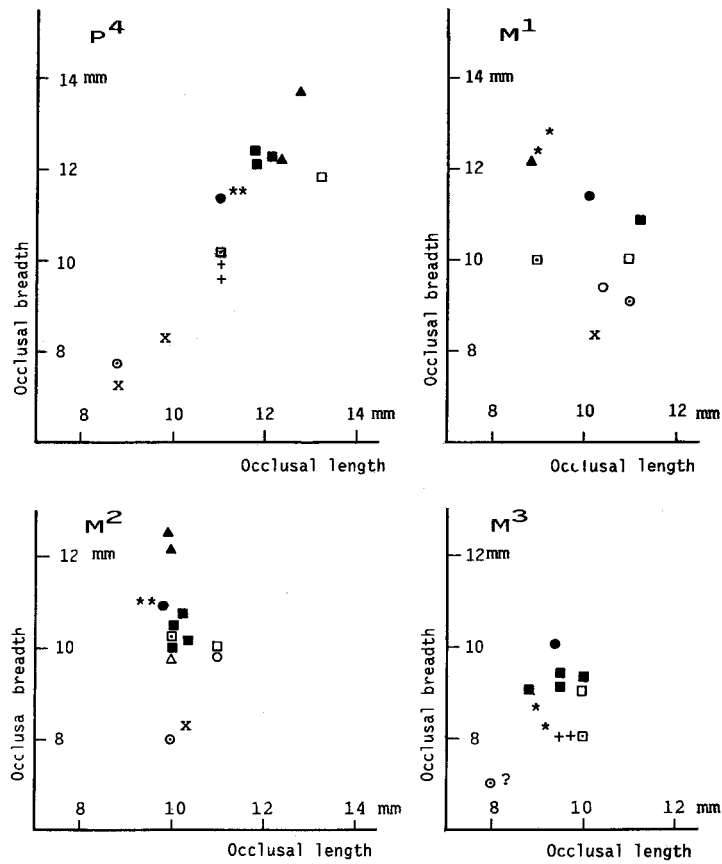


Fig. 3. Scatter diagram comparing the upper cheek teeth of various species of *Hystrix* from various localities.

Hystrix primigenia

- * DKO-41
- Pikermi, PMNH PIK 3116.
- Alifakas, Ath. No 1966/35; MELENTIS & SCHNEIDER (1966).
- Kalimanci; SEN & KOVATCHEV (1987).
- Weze; SULIMSKI (1960).
- △ Villaroya; AGUSTI et al. (1987).
- ▲ Layna; AGUSTI et al. (1987).

Hystrix major

- + Gerakarou 1, GER; KOLIADIMOU & KOUFOS (1991).
- x Venta Micena; AGUSTI et al. (1987).
- Valdarno; (BOSCO 1898).

Hystrix refossa

- St-Vallier; VIRET (1954).

Table 3. Upper cheek teeth dimensions of *Hystrix primigenia* from various European localities.

<i>Hystrix primigenia</i>													
Dytiko		Pikermi PMNH PIK-3116		Alifakas Ath. N° 1966/35 MELENTIS & SCHNEIDER (1966)		Kalimanci IV SEN & KOVATCHEV (1987)		Weze SULIMSKI (1960)		Villaroya AGUSTI et al. (1987)		Layna	
dex	sin	sin	sin	sin	n	min	mean	max	dex	dex	sin	dex	dex
P ⁴ - M ³	39.5	40.0	40.0	-	-	44.1	44.1	45.5	-	-	-	-	-
P ⁴ L	11.2	11.4	11.0	-	3	11.7	11.90	12.2	13.2	12.4	12.7	-	-
B	11.4	11.4	11.4	-	3	12.1	12.26	12.4	11.8	12.2	13.8	-	-
RI	101.7	100.0	103.6	-	3	100.8	103.1	106.0	89.4	98.4	108.7	-	-
M ¹ L	9.3	9.1	10.1	10.4	2	10.2	10.70	11.2	11.0	8.9	-	-	-
B	12.6	12.5	11.4	9.4	3	10.9	11.40	11.8	10.0	12.2	-	-	-
RI	135.5	137.4	112.9	90.4	1	97.3	97.3	90.9	137.3	-	-	-	-
M ² L	9.5	9.3	9.8	11.0	4	10.0	10.17	10.4	11.0	10.0	9.9	10.0	10.0
B	11.0	11.0	10.9	9.8	4	10.0	10.32	10.7	10.0	12.3	12.5	9.7	9.7
RI	115.8	118.3	111.2	89.0	4	97.1	101.5	105.0	90.9	123.0	125.7	98.6	98.6
M ³ L	9.1	9.0	9.4	-	4	8.8	9.45	10.0	10.0	-	-	-	-
B	8.2	8.5	10.0	-	4	9.0	9.17	9.3	9.0	-	-	-	-
RI	90.1	94.5	106.4	-	4	93.0	97.2	102.2	90.0	-	-	-	-

n = number of specimens; min = minimum observed value; max = maximum observed value; mean = mean value; PMNH = Museum Nationale d'Histoire Naturelle de Paris; L = occlusal length; B = occlusal breadth; RI = index Bx 100/L.

to the less attrition of Weze material. The number of the enamel loops and islets ranges from 6–7.

A cranial part from Taraklia was described under the name *Hystrix bessarabica* by RIABININ (1929). Despite the great similarity of this skull with that of *H. primigenia* from Pikermi, it was separated as new species because of the more complicated enamel pattern of the teeth. This species was later transferred to *H. primigenia* by SULIMSKI (1960). We agree with this because the above mentioned difference from the Pikermi material is due to the attrition.

Two isolated upper cheek teeth are known from the Pliocene locality of Roussillon (France) under the name *Hystrix primigenia* (DEPÉRET 1890, pl. 7, figs. 15, 16). The first tooth seems to be a M1, 2/ and the second a P4/. Their shape and enamel morphology fit with those of DKO-41 and Pikermi. *Hystrix primigenia* is also referred from two late Pliocene localities; a maxilla is known from Villaroya (Fig. 2f) and an isolated M2/ from Layna (AGUSTI et al. 1987). The teeth of Villaroya are very worn but their general shape of the occlusal surface, the number of the enamel loops and islets (4–6) and their proportions (Tab. 3, Fig. 3) are similar to those of Pikermi and DKO-41.

In the Villafranchian of Europe the story of hystricids is more complicated and many species such as *H. refossa*, *H. major*, *H. etrusca* are reported. Most of these species were erected by isolated incisors or few teeth and most of the morphological differences are due to the various stages of wear. Recently all the Villafranchian material has been included into the species *H. major* except that referred to *H. refossa*, because the known material is few and does not allow good comparisons. The main differences of *H. major* from *H. primigenia* are the smaller size (Fig. 3), the greater number of the enamel loops and islets (5–8), the more rounded lower cheek teeth, the more complicated synclinid I of the lower teeth and the more slender teeth (KOLIADIMOU & KOUFOS 1991). A well comparison of the DKO-41 teeth of *H. primigenia* is possible with the material of *H. major* from Macedonia ("Gerakarou 1", GER). Two P4/ and two M3/ are known from GER; they are smaller than those of DKO-41 (Fig. 3) with more enamel loops and islets (7) and more triangular-shaped M3/.

Conclusions

The determination and the taxonomy of the hystricids from the various European localities was mainly based on the enamel pattern of the occlusal surface of the teeth. However this pattern changes strongly with the attrition and the enamel loops are transformed into one or more islets. This gradual change of the enamel pattern gives the idea for a different species and for that reason the same species from the various localities has been described under various specific names. The change of the enamel pattern can be observed in the material from Kalimanci from where teeth of various stages of wear are known; the different enamel pattern in the teeth is clear (SEN & KOVATCHEV 1987, fig. 1).

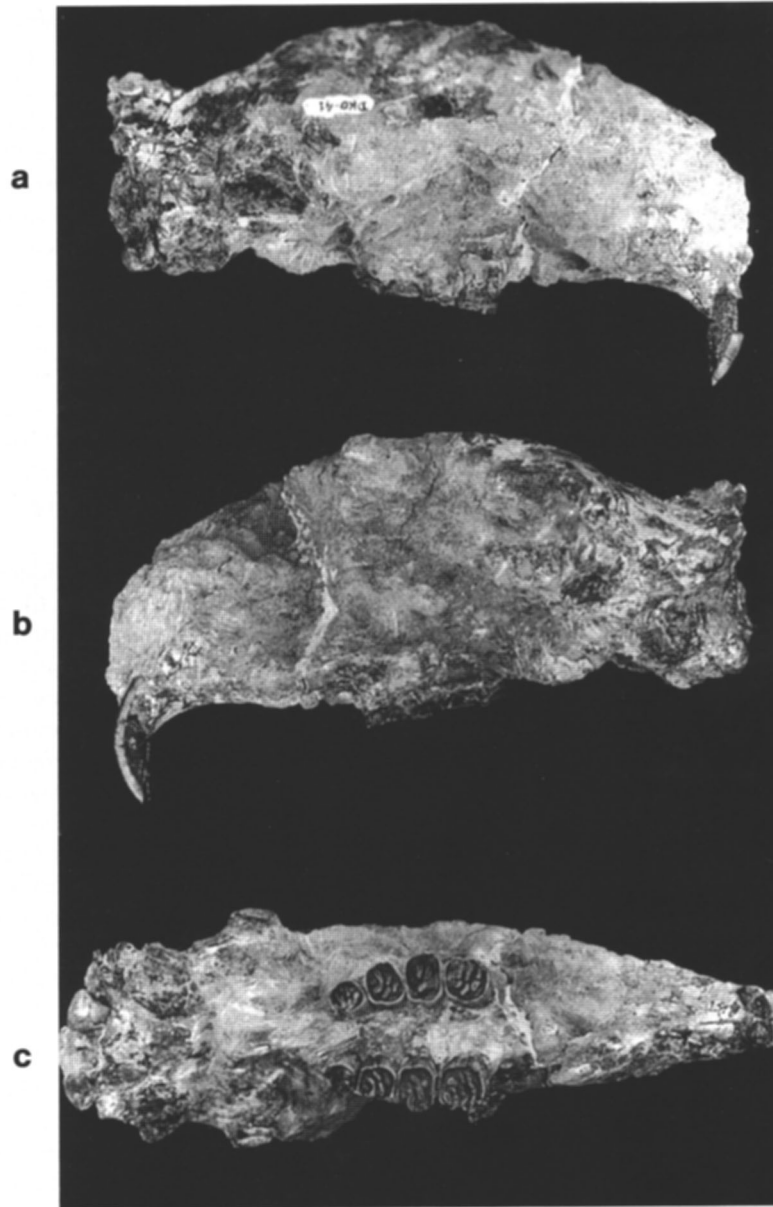
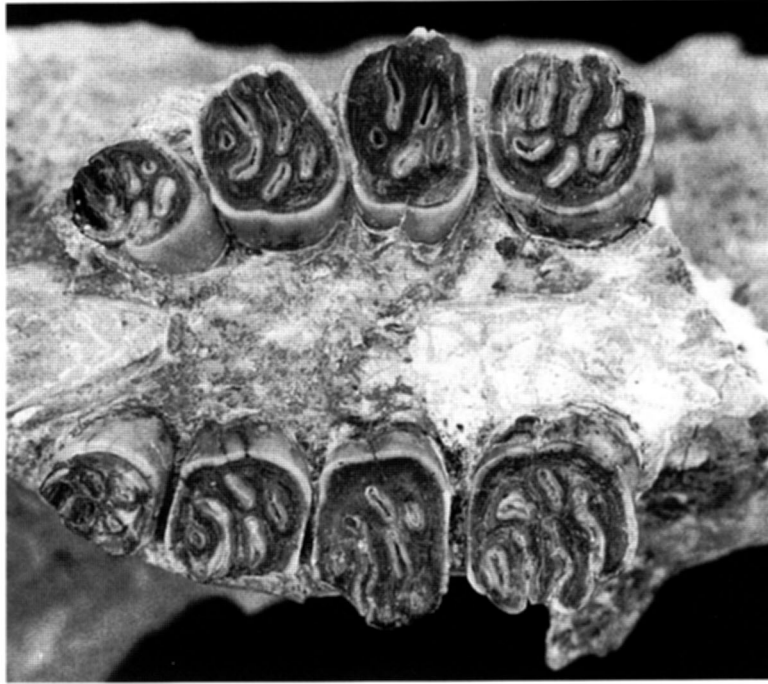


Fig. 4. *Hystrix primigenia*, "Dytiko 3", DKO, Macedonia, Greece. Skull, DKO-41; a. right lateral view, b. left lateral view and c. occlusal view. x $\frac{1}{2}$.



a



b

Fig. 5. *Hystrix primigenia*, "Dytiko 3", DKO, Macedonia, Greece.—a. Upper tooththrows of the skull DKO-41. x 2. b. Left upper incisor of the skull DKO-41; lateral view. x 1.

Moreover sometimes poor material (isolated teeth or incisors) were used for the erection of a new species. Thus the great number of the new species and the few material make difficult the taxonomy of the genus and we believe that more new material is necessary for better conclusions. The morphological and metrical comparison of Dytiko skull with the known hystricids from Europe show that it belongs to *Hystrix primigenia*. The species has a great stratigraphic range and it is referred from ? early Turolian (Halmyropotamos) to late Russonian (Weze). In Greece it is known from ? early Turolian, MN 11 (Halmyropotamos) until late Turolian, MN 13 ("Dytiko 3").

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