A porcupine skeleton of *Hystrix (Hystrix) primigenia* (Wagner) from the Upper Maeotian (Turolian) of Hadzhidimovo, SW Bulgaria

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Abstract. Relatively well preserved fossil skeleton of *Hystrix primigenia* (Wagner) is described. The locality near the town of Hadzhidimovo, Blagoevgrad district from which it was collected dated back as Late Maeotian, that is Turolian faunistic unit, MN12 zone. Comparisons are made with the bones of the modern species *Hystrix cristata* Linnaeus. It is concluded that it was a very large and adult animal whose characteristics strongly correspond to *Hystrix primigenia*. Some differences have been found which do not contradict to taxonomical assignment.

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Key words: Fossil porcupine, *Hystrix primigenia*, Maeotian (Turolian), Hadzhidimovo, SW Bulgaria, complete skeleton.

INTRODUCTION

The skeleton of a porcupine *Hystrix primigenia* here described was excavated in the summer of 1987 in the Girizite ravine, south of the town of Hadzhidimovo, Blagoevgrad district. It is situated 15 km south-east of the town of Gotse Dlechev in the Mesta Graben that is developed along the Mesta River. The paleontological site is located east of Sadovo village and north of Petrelik village.

The lithostratigraphy of the Miocene and Pliocene in the Gotse Delchev Basin was presented by Vatshev (1980) and Vatshev and Petkova (1996). Four formations were described from bottom to top: Valevitsa, Baldevo, Nevrokop and Sredna. The fossil porcupine here described from Hadzhidimovo locality was excavated from the Nevrokop Formation. The underlying Baldevo Formation crops out in the eastern and north-eastern part of the basin. This formation consists of silts, clays and sands, as well as diatomite levels and coal seams. Its age was determined as Pontian-Dacian on the basis of diatom and pollen analysis (Temniskova-Topalova and Og-

njanova-Rumenova, 1983; Ivanov, 1995; Yaneva et al., 2002; Ivanov et al., 2011).

The Nevrokop Formation is represented by conglomerates, sands, sandstones, siltstones and clays. It overlays the Baldevo Formation or lies directly on the Precambrian basement to the west. For decades, the Nevrokop Formation is famous with its rich and well preserved mammal faunas. Nikolov (1985) was the first to publish a list of fossil mammal species supposing a Maeotian age (MN12-13) of the Hadzhidimovo 1 locality. The fossil collection of this locality was made by D. Kovachev and is stored in the Paleontological Museum of Asenovgrad.

The first stratigraphic description of this area was provided by Nenov et al. (1972); Stoyanov et al. (1974). Modern data firmly indicated a Maeotian age, i.e. Turolian stage in terms of mammal stratigraphy, base of zone (Spasov, 2000, 2002). It may appear paradoxical than the Nevrokop Formation which in stratigraphic order is “over” is older in age than the Baldevo Formation. It is due to lateral thinning out of the Baldevo Formation westward where the base of Nevrokop Formation is directly on the Valevitsa Formation or on pre-Neogene rocks (see Vatshev, 1980).

SYSTEMATIC PART

Order Rodentia Bowdich, 1821

Family Hystricidae Burnett, 1830

Subfamily Hystricinae Lyon, 1907

Genus *Hystrix* Linnaeus, 1758

Subgenus *Hystrix* (*Hystrix*) Ellerman, 1940

***Hystrix* (*H.*) *primigenia* (Wagner, 1848)**

Locality. Girizite site, Hadzhidimovo Town, Blagoevgrad district, South-Western Bulgaria.

Age. Late Miocene, Maeotian; Turolian faunal unit, MN12 vertebrate zone (Spassov, 2002).

Material. An almost complete skeleton, hosted in the Asenovgrad Museum of Palaeontology, a branch of the National Museum of Natural History (NMNH) in Sofia, Bulgarian Academy of Sciences.

Museum No: HD 20 to HD 120.

DESCRIPTION AND COMPARISONS

Introduction

The taxonomy of the living species of the genus *Hystrix* is based on the differences in spiny covering and cranial features. Since the spiny covering does not fossilize and the finds of skulls are very rare, the taxonomy of the fossil Hystricidae is mainly based on the size of the cheek teeth. The latter are the most often found fossils.

Terminology

Description of teeth follows the terminology that according to van Weers (1985) was introduced by Modyer (1946) and Bossmma (1968). Nomenclature to describe the crown of the upper cheek teeth consists of a lingual concavity, sinus – hypoflexus, and three labial inflexions, namely paraflexus, mesoflexus and metaflexus. In advanced degree of development these inflexions transform into islets (or rings, or lakes) that are known as

parafoseta, mesofoseta and metafoseta, respectively. The lower molars, on the other hand, possess one labial and a few (normally three) lingual inflexions (synclinias) that are known as hypoflexid, paraflexid and metaflexid. When transformed into islets, the synclinias are called fossetidae.

Skull (Figures 1a-d, Table 1)

It is poorly preserved, flattened, the bones are broken. Some of them are absent. Maxillae and premaxillae are well preserved, as in some extent also platium durum and condylus occipitalis. The ventral part of the skull is better preserved.

Due to lateral pressure, the width of the skull is considerably changed. Its length is 189 mm measured from the labial part of the incisors to the posterior part of the condyli. This size is here accepted as normal of *H. primigenia*. Corbet and Jones (1965) reported values in the interval 118–170 mm for *H. cristata*. The skull of *H. cristata* (NMNH) is 165 mm long, i.e. smaller than the fossil skull of *H. primigenia*.

All teeth are found *in situ* and are perfectly preserved. Premaxillae are narrow and highly curved downwards. A small crest, 18 mm long, is seen on their antero-dorsal part. The same was previously observed by Niethammer (1982). *H. cristata* also possesses such a crest. A crest that is transversal to the maxillae was described by de Bonis et al. (1992) which is not observed in the studied here skull.

A small remain of acrus zigomaticus is seen on the left side of our skull. It is horizontal and starts from the middle of P4. The curving upwards is not observable as acrus zigomaticus is broken. Acrus zigomaticus in *H. cristata* starts much before the beginning of P4.

The nasal opening is of isosceles-triangular form, its base being upward. After fossa glenoidalis the braincase narrows and is almost cylindrical. Crista sagittalis is not preserved. Nasal bullae are fairly large. Their anterior margins are situated much behind the fossa glenoidalis. The same position was documented by de Bonis et al. (1992) in the skull of *H. primigenia* from Macedonia

Table 1
Measurements of skull (mm)

	<i>Hystrix primigenia</i>	<i>Hystrix cristata</i>
1. Length from the anterior end of I through the facial bones up to the posterior end of condyles occipitale	255	230
2. Length from the anterior end of I through the palate up to the posterior end of condyles occipitale	189	165
3. Length from the anterior field of the nasal cavities up to the connection between crista sagittalis and crista occipitalis	180	155
4. Length of the palate from the anterior end of I up to M3	113	91
5. Horizontal diameter of foramen magnum	19	17
6. Vertical diameter of foramen magnum	18	16
7. Distance between the anterior end of I up to the posterior end of M2	177	94
8. Distance between the anterior end of I up to the anterior end of P4	85	56
9. Distance between the anterior end of I up to the posterior end of M3	44	32.4

Fig. 1. Skull and mandible. Bar equals 5 cm
 a – skull and mandible, lateral view;
 b – lateral view;
 c – occlusal view;
 d – view from above.

district in Greece. Processus mastoides and processus paraoccipitalis are absent due to brokening.

Teeth formula $\frac{1\ 0\ 1\ 3}{1\ 0\ 1\ 3}$

Upper jaw teeth (Table 2)

The teeth rows are complete and well preserved. Due to lateral pressure the two teeth rows became closer. The primary divergence, however, is still preserved in some extent. The upper incisors are shorter, and rather strongly curved downwards than the lower incisors are curved upwards. Their roots reach close to the labial side of P4. Neithammer (1982) described the same features in the extant *H. cristata*. They have also been seen in *H. cristata* specimen from NMNH. The upper incisors are stouter than the lower ones. The antero-posterior diameters are 8.6 mm in the upper incisors, and 8.2 mm in the lower incisors. Their widths are 7.2 mm and 6.7 mm, respectively. Thus, the incisors are thicker than wide. The anterior surface is covered by completely smooth enamel, as is normally in all Hystricidae. The enamel embraces the incisors also laterally reaching the mid of their external sides and up to 1/3 of their internal sides. The color of enamel is yellow-brownish. Such increasing on enamel is a characteristic feature of the Hystricidae according to Koliadimou and Koufos (1990). The tips are grey-blackish in color due to manganese compounds. According to Malez (1963) the coloration varies depending on the host beds. Gaudry (1862) and Deperet (1890), however, considered that the yellow-brownish color of the incisors is typical for the porcupines in Pikermi. Deperet (1890) pointed out the triangle form of the upper and lower incisors. In our material the form is rather quadrangle, the posterior sides being curved and slightly shorter than the anterior ones. This makes them seemingly triangle. The well known vertical groove on the anterior side of the incisors that clearly separates their enamel is not deep and is hardly visible in HD-20. Harle (1910) compared his Quaternary material of the genus *Hystrix* with that of the genus *Castor*.

He emphasized on three main differences. In the genus *Hystrix* the enamel embraces the anterior side of the incisors reaching up to the mid of the lateral sides; the crest between the anterior and lateral sides is highly rounded; the cross section of the incisors of *Hystrix* is quite smaller than of *Castor*. J sup. sin et dex here described completely correspond to the above mentioned features of the genus *Hystrix*. Such is the case with *H. cristata* from NMNH.

A huge diastema separates J sup and P4 (Figs. 1a b). It is 70.4 mm long. All cheek teeth are excellently preserved. They are slightly longer and narrower than *H. primigenia* from Pikermi described by Gaudry (1862). The material from Hadzhidimovo possesses rounded sides and angles, the lingual surfaces being just slightly curved. Their size decreases from M1 to M3. Gaudry (1862) also considered the cheek teeth of *H. primigenia* as squarish.

P4 sin et dex. These are the longest cheek teeth (11.4 mm). The occlusal surface shows six enamel islets – fossetae, that originated from inflexions. Six enamel islets are largely reported in *H. primigenia* from other localities (see Sen, 1994). The morphology of islets corresponds to that described in *H. bessarabica* (= *H. primigenia*) from Taraklia. Riabinin (1929), however, mentioned the presence of three exterior grooves (inflexi), whereas in our material they are four in number. The third one is the deepest. The lingual side possesses only one groove. The latter gave rise of another groove (hypoflexus), just opposite to the third exterior one, the metaflexus. The hypoflexus and metaflexus divide the tooth into anterior and posterior parts. In the former, the pattern of the enamel figures (fossetae) is unclear. Four islets are seen. In the posterior part the islets are only two, one of them being “8”-shaped. A smaller islet is in front of it. The height of the P4 sin et dex could not be precisely estimated as the teeth were “pushed back” into the bone due to pressure. This does not allow a correct determination of the degree of hypsodonty. It should be added that these are the least worn teeth as they are the latest erupted.

M1 sin et dex. A small diastema (2 mm long) separates M1 sin et dex from the preceding P4. The both left and right cheek teeth are strongly worn and the two exterior enamel grooves (inflexi) are hardly visible. Vekua

Table 2
Measurements of the upper jaw teeth (mm)

		Length	Width	Height	Ratio H/L
Diastema I – P4	<i>H. primigenia</i>	70.4	–	–	–
	<i>H. cristata</i>	50.0	–	–	–
I	<i>H. primigenia</i>	8.6	7.2	–	–
	<i>H. cristata</i>	6.0	6.8	–	–
P4	<i>H. primigenia</i>	11.4	9.3	7.5	0.65
	<i>H. cristata</i>	8.7	6.0	2.0	–
M1	<i>H. primigenia</i>	10.0	9.0	4.0	0.40
	<i>H. cristata</i>	9.4	8.0	2.0	–
M2	<i>H. primigenia</i>	10.4	9.6	4.5	0.43
	<i>H. cristata</i>	9.5	7.5	2.0	–
M3	<i>H. primigenia</i>	9.0	8.5	5.3	0.58
	<i>H. cristata</i>	8.2	6.2	2.0	–

(1972) described a first molar with two inflexi, whereas that from Taraklia has only one inflexus (Riabinin, 1929). One hypoflexus is obvious on the lingual side. It reaches the base of the tooth crown, thus suggesting the presence of a hypoflexid. Each of the molars possesses five enamel islets. Only the most posterior one is rounded, the rest are worm-like. The material figured by Vekua (1972) shows a cheek tooth with seven fossetae, as the tooth was slightly worn. The roots are hidden in the bone and their number is not known. The tooth shape is slightly rounded rectangular, almost squarish. The labial sides are almost flat, and the lingual sides are more rounded. M1 in HD-20 shares same morphological features with the Pliocene Hystricidae. The width of M1 (HD-20) is similar to that of Weze, Poland, and Traklia, Moldova (Sulimski, 1960; Riabinin, 1929), and is smaller than that of Perpignan, France. Actually, Sen (2001a) described the Perpignan material as a new species, *H. depereti*. It should be noted that the described teeth are higher than all Quaternary and extant *Hystrix* from Africa and Asia.

M2 sin et dex. These cheek teeth share similar form and size with M1. Their extero-labial sides are more rounded and the lingual grooves are less expressed. These molars are slightly longer than M1. Their width is equal with *H. parvae* from Hohfidish, Austria (van Weers and Montoya, 1996). Two specimens of *H. aryanensis* from Molagan, Afganistan, described by Sen (2001 b) are as long as the material from Hadzhdimovo. Sen (1996) pointed out that in all specimens of *H. primigenia* except that from Weze, M1 is shorter than M2. Many authors considered this feature more expressed in the living porcupines *H. cristata* and *H. indica* (e.g. Sen and Kovatchev, 1987; de Bonis et al., 1992; Sen, 1996). Garevski (1956) mentioned that the first molars are the largest, and the last one – the smallest. Two well visible grooves could be seen on the labial side, and one groove – on the lingual side. The islets are four in number. All these features are same in the molar from Taraklia described by Riabinin (1929).

M3 sin et dex. These are the smallest upper cheek teeth. All angles are rounded. This gives an almost circular shape already mentioned in Pikermi, Kalimantsi and Weze (Gaudry, 1862; van Weers and Montoya, 1996; Sen and Kovatchev, 1987; Sulimski, 1960). The external and internal inflexi are hardly visible only on M3 dex. The porcupine *H. cf. primigenia* from Kvabebe, Georgia, has circle-shaped M3 (Vekua, 1972). The M3 have four roots. The lingual roots are fused, and the two labial roots are well shaped and separated.

The length of the upper teeth rows is 44 mm. This suggests that the described porcupine is a large-sized specimen. Greenwood (1955) considered that *Xenohystrix* described by him (teeth rows 40 mm long) is a large-sized Hystricidae. Our specimen is even greater. Actually, *Xenohystrix* is now considered as a junior synonym of *Hystrix* (van Weers, 1994).

Lower jaw (Table 3)

Only the two rami horizontali are preserved. Their lower surfaces are smoothly arc-shaped. This form is a result of the fact that the roots of the two lower incisors pass through the whole lower surfaces of the rami. Curving upwards, the crowns of the incisors form an angle of 40° with the alveolar row. The material described from Dytiko 3 in Greece (de Bonis et al., 1992) shows the same angle. Those authors concluded that, therefore, their Upper Miocene fossil is brachycephalous. Our specimen has a longer skull and is a large animal as a whole. Fossa masseterica reaches up to the labial sinus of m1. It has a well pronounced crista masseterica in its lower portion. Crista masseterica reaches to the posterior portion of p4 where it gradually disappears. The slightly inclined and less pronounced anterior margin of the coronoid appendice also goes to the posterior part of p4. Thus, fossa masseterica is embraced by another crista in its upper part. The height of the jaw is 23.5 mm at p4 and 27.0 mm at m3, i. e. it is slightly lower anteriorly. The thickness is 18.0 mm throughout its length. The length of the symphysis is 41 mm. Mandibular index is calculated as the height of the lower jaw between m3 and p4 multiplied ×100 and divided to the alveolar length between p4 and m3. According to Sen (1996) this index is quite indicative of the degree of teeth hypsodonty. The values of this index are 53.4 in three specimens of *H. primigenia* from Kalimantsi (Sen and Kovatchev, 1987), 56.3 in specimens from Pikermi and 78.5 in extant *H. cristata*. The described lower jaw has a mandibular index 54.4 that is rather close to the type material of Pikermi. As a whole, the degree of hypsodonty of fossil *H. primigenia* in Bulgaria and Greece is almost equal and significantly lower than living porcupines. The foramen mentale is large. It is open just in front of p4. A peculiar morphological feature of HD-21 is the presence of a second foramen, one centimeter behind the first one, right in the middle of p4.

When compared with *H. cristata* (NHNM, Sofia), the lower jaw (HD-21) of *H. primigenia* exhibits the following differences: 1) a steeper symphysis; 2) pars incisiva

Table 3
Measurements of the lower jaw (mm); * – broken bone

	<i>H. primigenia</i>	<i>H. cristata</i>
1. Length from the anterior part of I up to the posterior part of processus angularis	122.0*	123.0
2. Total length of the teeth raw I – m3	98.0	86.0
3. Length of p4 – m3	44.0	36.0
4. Height of ramus mandibuli through p4	23.5	26.0
5. Height of ramus mandibuli behind m3	27.0	29.0
6. Thickness of ramus mandibuli through p4	18.0	15.0
7. Thickness of ramus mandibuli behind m3	18.0	12.0

is not higher than the incisor alveolar margin; 3) fossa masseterica is shallower; a slight convergence anteriorly is hardly visible; 4) teeth rows are almost parallel; and 5) all teeth are shorter and thinner, arranged in arc rather than in a straight line.

Lower jaw teeth (Table 4)

All mandible teeth are excellently preserved. Due to lateral pressure the distance between them in the posterior end is obviously decreased. The pressure increased the divergence in anterior direction. This divergence is slighter in the upper jaw teeth.

The lower incisors have somewhat broken cutting edges. The cutting anterior faces are completely smooth. Grooves of varying depth, described by Sen (1994), are absent. This feature makes the material from Hadzhidimovo closer to extant porcupines. The lower incisors are much longer than the upper ones. The roots of the former pass under the roots of all cheek teeth thus forming an enlarged arc-shaped impression of the mandible, terminating right in its posterior end, immediately in front of the processus angularae. The latter is broken. Fortunately, this break reveals the interior of the two rami horizontali with the incisor roots inside. Koliadimou and Koufos (1990) mentioned that in *H. major* Gervais (= *H. refossa* Gervais) the incisor roots are shorter reaching up to m3. Compared to the upper incisors the lower incisors are seemingly gentle and elegant.

The diastema I – p4 is 56 mm long, i.e. rather shorter than the upper diastema I – P4. The cutting edges of the lower incisors do not reach those of the upper ones. Cutting tips of the lower incisors do not reach those of the upper incisors and remained significantly behind. Thus, they do not match.

p4 sin et dex. Sulimski (1960) showed a schematic drawing of the roots of all mandible teeth of *H. primigenia*. In that scheme, p4 has three sockets. Some authors suggest the presence of four alveoli. Our specimen of p4 sin has three short roots with shallow sockets. The occlusal outline is rounded rectangular. The buccal face has a deep sinus. It starts from the occlusal surface and reaches the roots (hypoflexidae). The sinus on the lingual side is

worn-out, almost invisible. This sinus is equivalent to the sinclinid that divides the teeth into two lobes – anterior and posterior. The former is longer and narrower than the latter. In the anterior lobe five enamel islands (fossetidae) are seen touching each other. Due to their complicated pattern, it is hard to determine which are the sinclinids giving rise to each islets. Four sinclinids are observed on the lingual faces of the incisors. The sinclinid IV occurs in the anterior lobe and is island-shaped (flexid).

m1 sin et dex. The occlusal surface is rectangular, 11.2 mm × 8.5 mm in size, and is slightly wider than p4. Koliadimou and Koufos (1990) stated that the margins, especially the lingual ones, are rounded. Vekua (1972) described a specimen of m1 which has rounded margins, too. In HD-21 they are less rounded. Vekua's (1972) material is wider than long. This is a rare exception. HD-21 is quite different. m1 teeth from Hadzhidimovo are characterised by seven enamel islands (fossetidae), whereas the Kvabebian fauna has only four. According to Koliadimou and Koufos (1990) the sinclinid I is much complicated and consists of a pair of small fossetidae and one „s“-shaped on the lingual edge. HD-21 has also a pair of enamel islets but one of them is considerably elongated and angular. The third one is „s“-formed, and enlarged in its end. The sinclinid II consists of two almost equal islets, one of them being minute and rounded. Sinclinid III is narrow and long. The axis of sinclinid IV is parallel to the lingual and labial enamel borders. Some authors stressed on the pyramide-like form of sinclinid IV which is not clear in our material. The teeth have four roots like the material from Weze (Sulimski, 1960) and not three roots like *H. cf. primigenia* from Kvabebe (Vekua, 1972).

m2 sin et dex. The anterior faces are straight, the rest are rounded. Angles are also rounded. The anterior margins are less rounded. The anterior lobe is slightly greater than the posterior one. The buccal sinuses are deep and oriented backwards. Among the lingual sinuses those related to the sinclinid III are almost transversal. The sinclinid III consists of three elliptical islets in the meso-lingual portion of the occlusal surface. The sinclinid II is similar in shape to m1. Sinclinid III, along with the buccal sinus, divide the occlusal surface into anterior and posterior

Table 4
Measurements of the lower jaw teeth (mm)

		Length	Width	Height	Ratio H/L
Diastema I – p4	<i>H. primigenia</i>	56.0	–	–	–
	<i>H. cristata</i>	46.0	–	–	–
I	<i>H. primigenia</i>	7.2	6.7	–	–
	<i>H. cristata</i>	6.0	5.4	–	–
p4	<i>H. primigenia</i>	10.6	8.5	9.2	0.86
	<i>H. cristata</i>	7.5	6.7	2.0	–
m1	<i>H. primigenia</i>	11.2	8.5	6.2	0.55
	<i>H. cristata</i>	8.0	7.0	2.0	–
m2	<i>H. primigenia</i>	10.5	9.6	7.0	0.66
	<i>H. cristata</i>	9.6	7.2	2.6	–
m3	<i>H. primigenia</i>	9.1	8.2	8.0	0.82
	<i>H. cristata</i>	8.2	5.0	2.0	–

lobes. The anterior one is greater. The sinclinal IV is an enlarged islet.

m3 sin et dex. Compared to the other molars, m3 have more expressed triangle occlusal surfaces. This is due to width decreasing in the posterior part. m3 teeth from Weze have same smaller width but the form is rounded. In 1890, describing his Pliocene *Hystrix* from Perpignan, Deperet wrote that m3 possesses better outlined triangle form than other lower cheek teeth but this difference is within the intraspecific variability. Thus, the porcupine from Perpignan was attributed to *H. primigenia*. Sen (2001 a), however, reexamined that material and attributed the bulk of it to the new species *Hystrix depereti*. One deep sinus passes through the labial portion of m3 (HD-21) from crown to roots. This sinus is oriented backwards. On the lingual face three deeply eroded sinclinals are seen. Riabinin (1929) wrote that m3 has two external grooves and three internal subdivisions of the enamel. There is a difference between our material and that from Taraklia. m3 has three relatively short roots.

To summarise, in *Hystrix* the order of eruption of lower and upper teeth is from front to back, like in all mammals: the incisors erupt first, followed by the premolars, and then the cheek teeth m1, m2 and m3 one after another. After the change of milk teeth P4, when the animal is one and a half years old, permanent P4 teeth erupt (Frenkel, 1970). For this reason, when all teeth are available (the case with HD-21), M1 is always the most worn. The attrition of the occlusal surface is slightest in P4. The latter are preserved as the highest teeth. This fact was described in 1890 by Deperet and is confirmed by our material. The cited author pointed out that the upper cheek teeth are more rounded than the lower ones. Again, HD-21 obviously reveals the same features. According to Frenkel's (1970) scale, the above described teeth from HD-20 and HD-21 correspond to class „D“ of high degree of attrition. All described teeth are yellow-brownish in color. Their sizes are similar to previously reported *H. primigenia*. Their slight hypsodonty, rather brachyodonty, together with other morphological features are also comparable to *H. primigenia* from other localities. If we accept Greenwood's (1955) concept that in the brachyodont teeth of the lower jaw in *Hystrix* the lower enamel boundary almost reaches the contact point between the crown and the roots, then the cheek teeth of HD-21 are brachyodont, indeed.

All Miocene porcupines of *Hystrix* are relatively lower-crowned, the ratio H/L of the molars being normally slightly greater than 1.0. These ratios of the molars from HD-20 and HD-21 are presented in Tables 2 and 4. All values are under 1.0 which means brachyodonty. One should remain, however, that all teeth are strongly worn and P4 are pushed back into the sockets. Thus, these results should be interpreted very cautiously. Van Weers and Montoya (1996) recognised that cheek teeth dimensions can not be taken to clear due to varying degrees of wear of teeth.

The onset of high-crowned porcupines like *Hystrix* occurred in the latest Miocene or Lower Pliocene (van Weers, 1996). Our material is in agreement with that as teeth material of Hadzhidimovo is older (MN12), of late but not latest Miocene age. Massini and Rook

(1993) were so deeply convinced in the brachyodonty of their Mondecian material that they assigned the teeth to *H. primigenia* mainly based on brachyodonty. Hadzhidimovo material is here also identified as *H. primigenia* considering the brachyodonty.

Following Greenwood (1955) concerning the number and development of the teeth roots, one diagnostic feature of *Hystrix* is that the upper molars are rootless. They only have small nodular roots and shallow alveoli. M3, m3 and p4 have also underdeveloped roots. Sulimski (1960) regarded the clear root differentiation of all teeth as a primitive characteristic.

Columna vertebralis (Table 5)

Thirty five vertebrae are relatively well preserved. Their distribution in groups is given below.

	<i>Hystrix primigenia</i>	<i>Hystrix cristata</i>
	Number of vertebrae	
Vertebrae cervicales	2	7
Vertebrae thoracales	14	14
Vertebrae lumbales	5	5
Vertebrae sacrales	5	5
Vertebrae caudales	9	7
Total	35	38

The table shows differences in the number of cervical and caudal vertebrae between *H. primigenia* and *H. cristata*. Five cervical vertebrae of *H. primigenia* were not found. The number of the caudal vertebrae indicates that the tail of *H. cristata* has two vertebrae less. This corresponds to Neithammer's (1982) description demonstrating that the tail of *H. cristata* is shorter, just 1/5 of the total length of thorax. This is due to the significantly shorter bodies (corpus vertebrae) of the caudal vertebrae (Table 5). The two species differ in the shape of spine. In *H. primigenia* the spine is convex upward in the area of the lumbar spine. Curve starts immediately after cervical spine, climbs quite steeply, and in the area of the lumbar spine slopes down to the sacrum. The latter is almost vertical. Seen from the side, the back of the porcupine has a hemispherical shape. In *H. cristata* the curve starts from the middle of the thoracic spine and is not as steep as in *H. primigenia*. The highest part of the arc is a little further back, near the sacrum which is shaped slightly concave arc.

Vertebrae cervicales(C1 – C7)

Atlas. This first cervical vertebra has preserved acrus anterior and arcus posterior. Its body was attributed to the second cervical vertebra, epistrophe, which was not found. All processes of the atlas are significantly damaged. There are only traces of the processus transversus

Table 5
Measurements of vertebrae (mm)

	Vertebrae	Thoracales	Lumbales	Sacrales	Caudales
<i>H. primigenia</i>	1	13.0	25	29	20
<i>H. cristata</i>	1	14.5	19	22	17.5
<i>H. primigenia</i>	2	16.0	27	28	23
<i>H. cristata</i>	2	15.0	23	22	17
<i>H. primigenia</i>	3	16.0	32	25	19
<i>H. cristata</i>	3	14.0	23	21	15.5
<i>H. primigenia</i>	4	16.0	29	24	20
<i>H. cristata</i>	4	15.0	24	19	13.5
<i>H. primigenia</i>	5	17.0	29	22	21
<i>H. cristata</i>	5	15.0	22	19	12.5
<i>H. primigenia</i>	6	17.5			23
<i>H. cristata</i>	6	15.5			11.5
<i>H. primigenia</i>	7	17.5			24
<i>H. cristata</i>	7	14.5			70
<i>H. primigenia</i>	8	17.5			20
<i>H. cristata</i>	8	15.0			
<i>H. primigenia</i>	9	19.0			19
<i>H. cristata</i>	9	14.0			
<i>H. primigenia</i>	10	19.0			
<i>H. cristata</i>	10	14.0			
<i>H. primigenia</i>	11	21.0			
<i>H. cristata</i>	11	15.5			
<i>H. primigenia</i>	12	22.0			
<i>H. cristata</i>	12	17.5			
<i>H. primigenia</i>	13	24.0			
<i>H. cristata</i>	13	17.0			
<i>H. primigenia</i>	14	24.0			
<i>H. cristata</i>	14	16.0			

sus. Only the right foramen transversarium is preserved. Foramen vertebrale has a very round shape. Its transversal diameter is 12 mm and the lateral diameter is 12 mm, too. Articular surfaces of the head and second vertebrae are well preserved. Only a fragment of the acrus vertebrae of the last cervical vertebra C7 has remained.

Vertebrae thoracales (Th1 – Th14)(Fig. 2a)

All 14 thoracic vertebrae are preserved. They have well-developed spinal processes. Spinal process of Th2 is longest, and that of Th1 is broken. All spinal processes are inclined backward. Forward to the posterior end this inclination increases and the length of spinal processes decreases. The last cervical vertebra Th14 is much like the lumbar spine. It differs from lumbar vertebrae in the presence of fovea costalis which serves as an articular connection with the corresponding rib bones. Each thoracic vertebra has two such fovea costalis except the first and last that only have one. Measurements of thoracic vertebrae are shown in Table 5.

Vertebrae lumbales (L1 – L5)

These are the largest vertebrae. They have developed corpus and transverse processes (processus laterales). These features clearly distinguish them from *H. cristata*. Spinal

processes are less developed and turned backward, opposite to the same processes in thoracic spine.

Vertebrae sacrales (S1 – S5)

These vertebrae are completely fused with each other to form a sacrum (os sacrum). Tops of the spinal processes retain their individuality but their bases are fused to form sacral crest (crista sacralis). This bone has a triangular shape. On the upper and lower surfaces, four paired openings (foramina sacralia pelvina) are merged to form highly elongated holes of the dorsal and ventral sides. This is certainly a result of deformation. Both sides of the sacrum, the right and left, are connected with the respective bones of the pelvis. Canalis sacralis passes along its entire length.

Vertebrae caudales (Cau1 – Cau 9)

Caudal vertebrae are two more in number than *H. cristata*. Although their sizes decrease towards the end of the tail, they remain much more massive than *H. cristata*. In the latter species, last caudal vertebra is strongly reduced, the length being 7 mm, and width – only 3 mm. It should be stressed that even the last caudal vertebrae are almost as long as the preceding ones in *H. primigenia*. Their processes are, however, atrophied, especially the lateral

ones. Same is true of their spinal processes, and the thickness of their bodies.

Rib bones (*ossa costae*)(Figs 2a, b; Table 6)

25 single rib bones are collected, 13 left and 12 right. The total number should be 14 pairs, as the number of the thoracic spines. The first pair of ribs are the shortest. The length of the following pairs of ribs increases to the sixth pair. Then, up to ninth pair they retain their

sizes. After the tenth pair of ribs their sizes decrease, but still remain larger than the first pair. Each rib has a head, caput costae, which has two articular surfaces intended to be connected to vertebrae. Exceptions are the first and last ribs which have only one such surface.

Skeletal elements of the fore limb (Figs. 3a, b)

Only the distal part of the left humerus was found. This bone is broken in the area of diaphysis. 35 mm of the

Fig. 2. Columna vertebralis and ribs. Bar equals 5 cm.
a – left ribs with thoracic vertebrae;
b – right ribs.

Table 6
Measurements of ribs (mm)

		Costae dextra		Costae sinistra	
		Length along the outer margin	Width at the curve of costae	Length along the outer margin	Width at the curve of costae
<i>H. primigenia</i>	1	110	11	80	–
<i>H. cristata</i>	1	40	14	37	14
<i>H. primigenia</i>	2	120	11	90	–
<i>H. cristata</i>	2	32	14	32	14
<i>H. primigenia</i>	3	125	12	110	–
<i>H. cristata</i>	3	75	17	74	17
<i>H. primigenia</i>	4	140	12	110	–
<i>H. cristata</i>	4	98	8.5	95	9.5
<i>H. primigenia</i>	5	154	10.5	115	–
<i>H. cristata</i>	5	115	9.0	115	9.0
<i>H. primigenia</i>	6	165	8.5	140	–
<i>H. cristata</i>	6	120	10.0	121	10.0
<i>H. primigenia</i>	7	168	11.3	150	–
<i>H. cristata</i>	7	135	7.9	138	7.5
<i>H. primigenia</i>	8	170	12.5	170	–
<i>H. cristata</i>	8	140	7.5	140	7.5
<i>H. primigenia</i>	9	175	9.5	170	–
<i>H. cristata</i>	9	142	7.0	142	7.0
<i>H. primigenia</i>	10	180	9.0	165	–
<i>H. cristata</i>	10	135	8.5	135	9.5
<i>H. primigenia</i>	11	170	9.2	165	–
<i>H. cristata</i>	11	135	8.0	135	8.0
<i>H. primigenia</i>	12	155	9.2	130	–
<i>H. cristata</i>	12	110	6.0	110	6.0
<i>H. primigenia</i>	13	–	–	115	–
<i>H. cristata</i>	13	–	–	110	6.0
<i>H. primigenia</i>	14	–	–	–	–
<i>H. cristata</i>	14	–	–	108	6.0

lower portion of tuberositas deltoidea are preserved. It shows that this process reaches up to 57 mm above the lower end of the trochlea. Condilus medialis and condilus lateralis are perfectly preserved. The same is true for the two crests which derive from them. Medial crest is sharper.

Measurements (mm) of this femoral fragment as compared with the same bone in *H. cristata* are given in the table below. Diameters of diaphysis are measured at the bottom of tuberositas deltoidea.

	<i>H. primigenia</i>	<i>H. cristata</i>
1. Length of the preserved part	97	–
2. Antero-posterior diameter of diaphysis	27	21
3. Lateral diameter of diaphysis	12	11
4. Antero-posterior diameter of distal epiphysis	23	12
5. Lateral diameter of distal epiphysis	40	35

Skeletal elements of the hind limb

Pelvis (Fig. 4a; Table 7)

It consists of three bones – sacrum (os sacrum), and two hip bones (ossa coxae). All three bones are present although slightly damaged. Pelvis is larger and more upright than *H. cristata*. All three parts of ossa coxae are preserved. Flank bone (os ilium) builds broader anterior part of the bone. It is slightly concave compared with that in *H. cristata*. Seatbone (os ischii) builds the back of the pelvis. Tuber ischiadicum which is located on the curvature of the backbone is much more developed than *H. cristata*. Pubic bone (os pubis) builds frontal part. It is broken in both nameless bones.

Femur (Fig. 4b; Table 8)

Both left and right hipbones are preserved. These are the longest skeletal elements. They are much more solid, longer and more flattened than *H. cristata*. In both *H. primigenia* and *H. cristata* hipbones are quite right. In many mammals they are more or less curved. Proximal epiphysis has a head (caput femori) with underdeveloped fovea capitis femori. Neck (collum femori) is not very

long and makes an angle of 130° with the hipbone body (corpus femori). Trochanter major has a lateral position, and trochanter minor is placed in medial position and beneath the neck; between the two trochanters is crista trochanterica.

All these skeletal details form fossa trochanterica, a pit of rounded triangle outline. Trochanter major rises 11 mm over caput femori. Diaphysis is completely smooth and third trochanter, trochanter tercius, is observed as in *H. cristata*. Fossa suprapatellaris is barely noticeable.

Fig. 3. Skeletal elements of the limb. Bar equals 5 cm except stated otherwise.
a, b – humerus, distal part; a – frontal view; b – view from behind;
c, d – patella; c – frontal view; d – view from behind;
e – m – bones of the metacarpus; e, g, i, l – frontal view; f, h, k, m – view from behind; bar equals 1 cm in i, k, l, m.
n, o – carpus and metacarpus (I, II and III); n – dorsal view; o – planar view.

a

Fig. 4. Skeletal elements of the hind limb. Bar equals 5 cm.

a – pelvis, view from below;

b, c – left femur; b – frontal view; c – view from behind;

d, e – right femur; d – frontal view; e – view from behind.

Table 7

Measurements of the pelvis (mm)

	<i>H. primigenia</i>	<i>H. cristata</i>
1. Length of the preserved part	165	154
2. Antero-posterior diameter of the acetabulum	28	21
3. Vertical diameter of the acetabulum	26	19
4. Ratio length of pelvis/length of skull	1/1.1	1/0.67

Table 8
Measurements of the long bones of the hind limb; * – slightly damaged

	Femur				Tibia			
	<i>H. primigenia</i>		<i>H. cristata</i>		<i>H. primigenia</i>		<i>H. cristata</i>	
	sin	dex	sin	dex	sin	dex	sin	dex
1. Total length of the bone	157	157	128	129	152*	154	116	115
2. Proximal epiphysis								
a) transversal diameter	51	50	39	39	39	39	30	30
b) antero-posterior diameter	20	21	19	19	30	30	20	20
3. Diaphysis								
a) transversal diameter	22	22	15	15	14	14	10	10
b) antero-posterior diameter	15	15	15	14	17.5	17.5	12	11.8
4. Distal epiphysis								
a) transversal diameter	36	36	31	31	28	28	22	22
b) antero-posterior diameter	40	41	34	37	21	20	14	12
5. Diameter of caput femori	21	21	18	18	–	–	–	–

***Tibia* (Figs 5a, b)**

As with the femur, at the left and right tibia the site of the cartilage (cartilago epiphysialis) is between the metaphysis and epiphysis. Increase in bone length is achieved through this cartilage. Proximal epiphysis is formed of condylus medialis and condylus radialis. Each of these has a joint surface with the femur. In their midst is seen outlined eminentia intercordilaris. Diaphysis, corpus tibiae, is triangular. The distal epiphysis ends with a well-preserved joint surface for connection to plantar bones, i.e. the tarsus. Measurements of tibia are shown in Table 8. It indicates equal lengths of the femur and tibia. By contrast, in *H. cristata* tibia is shorter than femur.

***Ossa pedis* (bones of the foot)**

Bones of the foot of the left limb are better preserved. A part of them are missing. If one combines them with

the preserved bones of the right limb, a “complete” ossa pedis is formed consisting of tarsus, metatarsus and phalanges.

Tarsus (Table 9). It includes calcaneus, astragalus, naviculare, cuboid and three cuneiformes, namely ecto-, meso-, and endocuneiforme. Measurements of all these skeletal elements are given in Table 9.

Calcaneus sin. It lies in the lower part of the foot. Its back part, tuber calcanei, is 28 mm long. It associated with the Achilles tendon without a visible groove of this coupling. Sustentaculum is in medial position supporting the astragalus and bearing one of its three articulating surfaces. Only one of them is slightly concave. The three surfaces are divided by sulcus calcanei. The plantar surface of tuber calcanei is damaged. The big processus of calcaneus is truncate in a manner that the head of astragalus is well seen at the distal end of calcaneus. A large fasseta for the cuboid occurs at that end. The fasseta is slightly concave.

Table 9
Measurements of the tarsus (mm)

		Antero-posterior diameter	Transv. diameter	Transv. diameter at trohlea	Transv. diameter at head	Length of sustentaculum up to the free end	Vertical diameter
calcaneus	<i>H. primigenia</i>	48.0	27.0	–	–	40.0	–
	<i>H. cristata</i>	36.0	19.0	–	–	31.0	–
astragalus	<i>H. primigenia</i>	27.5	–	21.0	11.0	11.0	–
	<i>H. cristata</i>	20.0	–	18.0	8.0	8.0	–
naviculare	<i>H. primigenia</i>	19.5	12.5	12.5	–	–	12.5
	<i>H. cristata</i>	11.5	11.5	12.0	–	–	12.0
endo-cuneiform	<i>H. primigenia</i>	19.0	12.5	–	–	–	12.5
	<i>H. cristata</i>	15.5	12.5	–	–	–	12.0
meso-cuneiform	<i>H. primigenia</i>	10.0	7.0	5.0	–	–	5.0
	<i>H. cristata</i>	–	–	–	–	–	–
ecto-cuneiform	<i>H. primigenia</i>	–	–	9.0	–	–	9.0
	<i>H. cristata</i>	9.0	11.5	–	–	–	–
cuboid	<i>H. primigenia</i>	15.5	17.2	10.0	–	–	16.0
	<i>H. cristata</i>	12.0	12.5	10.0	–	–	10.0

Fig. 5. Skeletal elements of the hind limb. Bar equals 5 cm.
a, b – right tibia; a – view from the front; b – view from behind;
c, d – left tibia; c – view from the front; d – view from behind;
e, f, g – tarsus and metatarsus; e – dorsal view; f – lateral view; g – planar view

Astragalus sin. All its components are well preserved – caput, colum and corpus. Head is oval. Its transversal diameter is 18 mm and the vertical diameter is 11 mm. At the distal surface there is a large convexe fasseta for coupling with naviculare. At the upper surface of the corpus trochlea occurs with three shallow surfaces for articulation with the tibia. The inner condylus is slightly higher than the outer. In plantar view, there are also three articulation surfaces of calcaneus which are divided by sulci. The two bones, calcaneus and astragalus, have been found connected.

Naviculare sin. It is boat-shaped, flat and relatively thin. It becomes higher in medial direction. The upper end is boat-shaped concave and forms a fasseta for the astragalus. The postero-external apophysis is significantly elevated. On the internal side there is a fasseta surving for connection with the cuboid. It is connected with the cuneiform bone through its plantar part.

Endocuneiform dex. This bone is long and highly flattened laterally. Its dorsal diameter is smaller than the plantar one. The bone is positioned over Mt – I by a highly concave fasseta. Such a fasseta also exists on the proximal surface making connection with the naviculare, however, this fasseta is not concave. On the fibular surface there are two fassetae – one proximal for the mesocuneiform, and other, smaller distal fasseta for Mt – II.

Mesocuneiform dex. Its antero-posterior diameter is larger than the transversal diameter, especially on the distal surface. The fasseta for connection with naviculare is tilted back and remains flat throughout its length. In the distal part this bone is elevated by Mt – II.

Ectocuneiform sin et dex. This is the largest of the three cuneiforms. It lies entirely over Mt – III and is apparently wider than tall. Its distal fasseta for connection with Mt – III is strongly sloped. In dorsal view, it just lies on its fibular top creating an impression of diamond-shaped. This impression is reinforced by the fact that the lateral surfaces are shorter than the anterior and posterior ones.

Two fassetae are seen on the fibular surface – one for the mesocuneiform, and other, distal for Mt – II.

Cuboid sin et dex. Cuboid is situated on the lateral side of foot, just opposite to the anterior surface of the calcaneus. The dorsal surfaces are slightly concave in proximal direction. The proximal surface connects the cuboid with the calcaneus; it is flat and highly tilted forward. This slope rapidly disappears laterally. At the distal end of this bone, a large fasseta connects it with the proximal ends of Mt – IV and Mt – V.

Metatarsus (Figs 5e, f, g; Table 10). Metatarsus dex is completely preserved. Metatarsus sin is represented by its Mt – III, and the proximal parts of Mt – IV and MT – V.

Metatarsus – I dex. It is situated at medial position and represents the greatly reduced metatarsus. Its head is highly enlarged compared to both antero-posterior and transversal dimensions. For this reason, the fasseta on endocuneiform is also large. It is sloped and thus the first finger points inward. The form is arc-shaped, slightly convex forward. The distal trochlea is hemispherical.

Metatarsus – II dex. The connecting surface with mesocuneiforme is short and slightly concave. The head is elevated over the heads of Mt – I and Mt – III. In dorsal view, the body of bone is quite straight, whereas in plantar view it looks arc-shaped, convex upwards. This impression is reinforced by the larger antero-posterior diameters at its both ends. The corp has a form of highly flattened cylindre, widened at its ends. In distal direction, the bone widens transversally. The dorsal surface of trochlea is sphaeroidal; the plantar surface is divided into two parts by a crest, a structure which is seen in all metatarsalia.

Metatarsus – III sin et dex. It is slightly longer than Mt – II. The antero-posterior diameter of its head is longer than Mt – II. The fasseta to connect with the ectocuneiforme is strongly sloped. To connect with Mt – IV the bone head is deeply concave and overthrusts the head of Mt – IV. The diaphysis is slightly more massive than Mt – II. In dorsal view it is quite straight, whereas in plantar view

Table 10
Measurements of the metatarsus (mm)

			Length of bone	Antero-posterior diameter of head	Transversal diameter of head	Transversal diameter of the distal end
Mt-I	<i>H. primigenia</i>	sin	20	9.0	8.5	6.8
		dex	–	–	–	–
Mt-II	<i>H. cristata</i>	sin	–	–	–	–
		dex	–	–	–	–
Mt-III	<i>H. primigenia</i>	sin	36.5	–	9.0	9.0
		dex	–	–	–	–
Mt-IV	<i>H. cristata</i>	sin	27.5	14.0	–	5.5
		dex	–	–	–	–
Mt-V	<i>H. primigenia</i>	sin	41.5	–	12.0	10.5
		dex	45.0	12.5	10.5	11.5
Mt-VI	<i>H. cristata</i>	sin	31.0	10.0	8.0	8.0
		dex	–	–	–	–
Mt-VII	<i>H. primigenia</i>	sin	39.5	14.0	12.0	10.5
		dex	–	12.0	10.0	–
Mt-VIII	<i>H. cristata</i>	sin	31.0	9.0	6.0	7.0
		dex	–	–	–	–
Mt-IX	<i>H. primigenia</i>	sin	38.0	11.0	17.0	10.0
		dex	–	9.0	17.0	–
Mt-X	<i>H. cristata</i>	sin	29.0	10.0	7.0	8.0
		dex	–	–	–	–

the diameter is smaller than the lateral diameter. Thus, the bone looks oval and flattened. The distal epiphysis is similar to Mt – II, but is clearly more symmetrical.

Metatarsus – IV sin et dex. Its shape and dimensions are equal to MT – III. The only difference is that the connecting fasseta to the cuboid is less tilted. Mt – IV is represented by only its head and a part of diaphysis.

Metatarsus – V sin et dex. It is slightly longer than Mt – II. This bone is more flattened than the other metatarsalia. In transeversal sections its diaphysis looks oval and flattened. The head is strongly tilted outward and upward. The fasseta over the head curves in the same direction in order to articulate with the cuboid. Mt – V dex is only represented by its proximal part (head and part of diaphysis) which show no differences with the well preserved Mt – V sin.

Sesamoidal bones. There is only one preserved sesamoidal bone from this group, beside the pattela of the left limb which is a part of the knee. This single bone was found lying between the distal trohlea of MT II and the proximal fasseta of the first bone of second finger. Patella has a characteristic crescent-shaped outline and is very small in size.

Phalanges dex (Table 11)

Only fingers of the right hind leg are found. These are five in number. Each finger has three ossicles, namely proximalis, medialis and distalis. The first finger only has two ossicles. Proximal ossicles are the longest and distal ossicles are the shorter. Their arched shape is more obvious than metatarsalia. Proximalia of all fingers are flattened dorso-ventrally. They have a concave pit to articulate with the corresponding metatarsus. The distal part of this pit is the trohlea which surves for connection with the medial ossicle of the finger. These second phalanges resemble the proximal ossicles, however, being slightly shorter. The third phalanges (distalis, the nails) are highly thickened in proximal direction. The presence of a big tuber on their plantar surface contributes to this impression. The third phalanges are arc-shaped upwards. They do not sharpen to the distal end as might be expected. Their distal ends are as thick as the beginninig of diaphysis. These nails have had likely a reactive character. They came back to the distal ossicles when not used. This assumption is based on the presence of a deep pit on the nails dorsal surface. Such a device, much more sophisticated, of course, is seen in cats. Pits similar but much shallower can be seen in the extant species *H. cristata*.

As a whole, in the majority of metatarsus and phalanges bones grooves are visible (in places clearly) where

Fig. 6. Image of living *Hystrix cristata* Linn

cartilage plates (cartilago epiphysalis) passed before completely ossified.

The description, measurement and comparison of the fossil material suggest that the skeleton of Hadzhidimovo locality was a quite big animal which univocally belongs to *Hystrix primigenia*.

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION

The stratigraphic range of *Hystrix* (*H.*) *primigenia* was summarised by Alcalá and Montoya (1998), van Weers and Rook (2003) and Lopatin et al. (2003). The stratigraphic range of the species is from the early-middle Turolian (transition MN 11/12) to the late Ruscinian (MN 15). *H. primigenia* was reported so far from the following localities in Europe:

Greece: Pikermi, Samos, Chomateras, Palmyopotamus, all four localities middle Turolian in age (MN 12) and Dytico – late Turolian (MN 13) according to de Bonis et al. (1992); Koufos (2006); Koufos et al. (2011)

Albania: late Miocene to early Pliocene (Festani et al., 1997);

FYR Macedonia: Umen Dol, (Garevski, 1956);

Turkey: Kemiklitepe, Turolian (MN 11, MN 12) (de Bonis et al., 1994), also Bayirköy, Gülpınar, Şerefköy;

Moldovia: Taraklia (Riabinin, 1929) as *H. bessarabica*, a junior synonym of *H. primigenia*;

Table 11

Measurements of the phalanges (mm); *H. pr.* = *Hystrix primigenia*, *H. cr.* = *Hystrix cristata*

	1		2		3		4		5	
	<i>H. pr.</i>	<i>H. cr.</i>	<i>H. pr.</i>	<i>H. cr.</i>	<i>H. pr.</i>	<i>H. cr.</i>	<i>H. pr.</i>	<i>H. cr.</i>	<i>H. pr.</i>	<i>H. cr.</i>
Length of the I phalange	–	17.0	32.0	13.0	42.0	15.0	40.0	15.0	30.0	15.0
Length of the II phalange	14.0	8.5	10.0	7.0	12.0	8.5	19.0	9.0	16.0	9.0
Length of the III phalange	9.0	7.5	14.0	12.0	13.0	10.0	17.0	12.0	15.6	11.0

European Russia: Morskaya 2, late Turolian (MN 13) (Lopatin et al., 2003);

Poland: Weze, early Pliocene, Ruscian (MN 14) (Sulimski, 1960);

Italy: Brisighella, latest Miocene (Masini and Rook, 1993);

Spain: Las Casiones (Alcala and Montoya, 1998);

Algeria: Menacer, late Miocene (see van Weers and Rook, 2003);

India: As *H. sivalinsis* Lydekker, a junior synonym of *H. primigenia* (Sen, 2001 b);

Bulgaria: Kalimantsi, Struma River Basin, SW Bulgaria, MN12 (Sen and Kovachev, 1987); Strumyani, Struma River Basin, SW Bulgaria, MN 12 (Geraads et al., 2011). The first description of *H. primigenia* from Hadzhidimovo locality was by Kovachev and Atanasova (2008). Spassov (2000) mentioned this species in the faunal list of Hadzhidimovo I locality.

Vekua et al. (2010) argued that the specimen reported earlier as *H. cf. primigenia* by Vekua (1972) from Kvabeba locality in Georgia resembles *H. primigenia* but is not well preserved for reliable identification. The age of Kvabeba locality is, however, lower Villafrankian (MN 16). All other localities of *H. primigenia* in Europe, Asia Minor and North Africa are up to the late Ruscian in age (MN 15).

Van Weers and Rook (2003) made a taxonomical revision of the late Miocene (Turolian) and early Pliocene (Ruscian) large-sized fossil porcupines and allocated them in the subgenus *Hystrix* (*Hystrix*). Those authors considered *Hystrix syvalinensis* Lydekker and *Hystrix besarrabica* Riabinin as junior synonyms of *H. primigenia*. *H. syvalinensis* was reported from Siwalkis, India, by Sen 2001b, and *H. bessarabica* – from Moldova by Riabinin (1929), both from the Turolian.

Other Miocene and Early Pliocene fossil species of large porcupines (*Hystrix*) of Europe, Asia Minor and Middle East are:

Hystrix parvae (Kretzoi, 1951)

Hystrix depereti Sen, 2001a

Hystrix aryannensis Sen, 2001b

Hystrix caucasica (Argyropulo, 1939)

H. (H.) parvae is a small porcupine which appeared before *H. primigenia*. It is known from the latest Vallesian (MN 10) and Early Turolian (MN 11) of Europe. The locality Kohfidish in Austria which was thought to be Late Vallesian (MN 10) in age was recently dated as Early Turolian (MN 11) by Daxner-Höck and Höch (2009). *H. (H.) suevica* Schlosser, 1884 is a junior synonym.

H. (H.) depereti was first described from the classical material of Perpignan, France. This is the closest fossil species to *H. primigenia*. The stratigraphic range of *H. depereti* is slightly younger than *H. primigenia*. Van Weers and Rook (2003) re-examined fossil collections and considered that the material previously described as *H. primigenia* from Samos Island in Greece, Çoban Pınar in Turkey, Kalimantsi in Bulgaria, Weze in Poland, Brisighella in Italy, Las Casiones in Spain, and Menacer in Algeria, should actually be allocated to *H. depereti*. Lopatin et al. (2003) did not accept that and maintained the name *H. depereti* only for the material of Perpignan, France.

H. (H.) aryanensis Sen is known from its type locality Molayan, Afganistan, in the Middle Turolian (MN 12) (Sen, 2001b). Later it was also documented in the Ivand locality, Iran, by Sen and Purabnishi (2010) again from the Middle Turolian (MN 12).

Hystrix caucasica (Argyropulo) from Kolyakino locality in Northern Caucasus is from the early Ruscian (MN 14) (Lopatin et al., 2003).

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