



Research Article

The earliest *Hystrix refossa*: a new Early Villafranchian record from Milia (Grevena, Macedonia, Greece)

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Abstract

From the Early Villafranchian site of Milia (Grevena) in northern Greece a mandible fragment of a porcupine with part of the incisor has been recorded. Despite its fragmentary nature, morphologically the fossil has been referred unambiguously to the genus *Hystrix*; according to various size parameters it belongs to the species *H. refossa*. A compilation of all known porcupine fossils attributed to this species indicates that the find from Milia is the oldest record of *H. refossa* so far, the age of which is correlated with the early part of the informal Mammal Sub-Zone MN 16a. Age and location of the record suggest that — in parallel to the preceding species *H. primigenia* and *H. depereti* — the porcupine species *H. refossa* spread from south-east Europe (Balkans) eventually over Europe. The Milia porcupine presumably inhabited vegetated river banks within a mosaic of open and forested terrain under warm and humid conditions.

Introduction

Fossil remains of porcupines of the genus *Hystrix* are not rare in Europe, considering the fact they are known from about 150 Neogene and Quaternary sites. However, their spatial and temporal distribution is uneven. Records are concentrated in particular regions and time intervals and are less frequent in others. Their occurrences in Europe cover a total time span of approximately ten million years.

Nowadays, so-called old world porcupines (family Hystricidae, including the genera *Trichys*, *Atherurus* and *Hystrix*) inhabit a huge area from Africa to south-east Asia with 11 (Wilson and Reeder, 2005), respectively 12 (Van Weers, 2005) species. South-east Asia displays the highest diversity of extant hystricid species, and was therefore often suspected to be the evolutionary centre of this group (Van Weers, 2005). Although the most primitive extant porcupine *Trichys fasciculata* (Shaw, 1801) is an exclusively south-east Asian species, until now, only one fossil remain of a hystricid has been found in this region older than of Pleistocene age (see below). By contrast, an African origin of porcupines can be deduced from the exclusively African rodent family Gaudeamuridae (Eocene – Oligocene), the possible sister group of Hystricidae; the molecular divergence between the groups is estimated to have occurred at 39 Ma BP (Late Eocene) (Barbière and Marivaux, 2015; Sallam et al., 2011). Currently, the only species occurring in Europe is *Hystrix cristata* (Linnaeus, 1758), and supposedly it was introduced by man (Wilson and Reeder, 2005).

The oldest fossil record that can be clearly referred to hystricids is an 11 Ma old find from Egypt (Mein and Pickford, 2010). Slightly younger fossils belonging to the small-sized species *Hystrix parvae* Kretzoi, 1951 have been identified from European Land Mammal Zone MN 10

(Late Miocene; Late Vallesian; 9.5–9.0 Ma) (here and henceforth, absolute ages after Hilgen et al., 2012) and MN 11 (Late Miocene; Early Turolian; 9.0–8.2 Ma) in Spain, Germany, Austria, and Hungary (Van Weers and Montoya, 1996) (Fig. 1). The stratigraphically younger and larger species *H. primigenia* (Wagner, 1848) is known from MN 11–MN 13 (Turolian; 9.0–4.7 Ma) at 25 European sites (Van Weers and Rook, 2003). *H. depereti* Sen, 2001, (Sen, 2001b) has been reported from various European sites ranging in age from MN 12 (Middle Turolian; 8.2–7.0 Ma) to MN 15 (Early Pliocene; 4.2–3.4 Ma) (Van Weers and Rook, 2003). It is even larger and its molars are more high-crowned than in *H. primigenia*. However, Lopatin et al. (2003) consider the samples mentioned by Van Weers and Rook (2003) as statistically unreliable for a numerical distinction, and thus restrict the unambiguous record of *H. depereti* to the type locality Perpignan in France (MN 15b). Other Miocene species are the exclusively Asiatic species *H. aryanensis* Sen, 2001, from the Middle Turolian of Afghanistan (Sen, 2001a) and Iran (Sen and Purabrishemi, 2010), *H. gansuensis* Wang and Qiu, 2002 and *H. lufengensis* Wang and Qi, 2005 from the Late Miocene of China (Van Weers, 2005), and *H. paukensis* Nishioka et al., 2011 from the Late Miocene/Early Pliocene of Myanmar (Nishioka et al., 2011).

The Plio-Pleistocene species *H. refossa* (Gervais, 1852) is known from some 50 sites in Europe, Asia, and Africa from MN 16 to the Late Pleistocene. According to Van Weers (2005, 1994), the following names are synonyms: *H. major* Gervais, 1859; *H. crassidens* Lydekker, 1886; *H. etrusca* Bosco, 1898; *H. angressi* Greenwood, 1958; *H. makapensis* Frenkel, 1970; *H. gigantea* Van Weers, 1985; and *H. magna* Pei, 1987. The small-sized *Hystrix vinogradovi* Argyropoulos, 1941, mentioned from c. 50 European Pleistocene sites, is considered by Van Weers (2005) as a synonym of the extant *Hystrix (Acanthion) brachyura* Linnaeus, 1758, whereas other authors consider *H. vinogradovi* as a separate species (Vekua et al., 2010; Salari and Sardella, 2009; Maul, 1994; Mottl, 1967; Jánossy, 1964) or subspecies *H. bra-*

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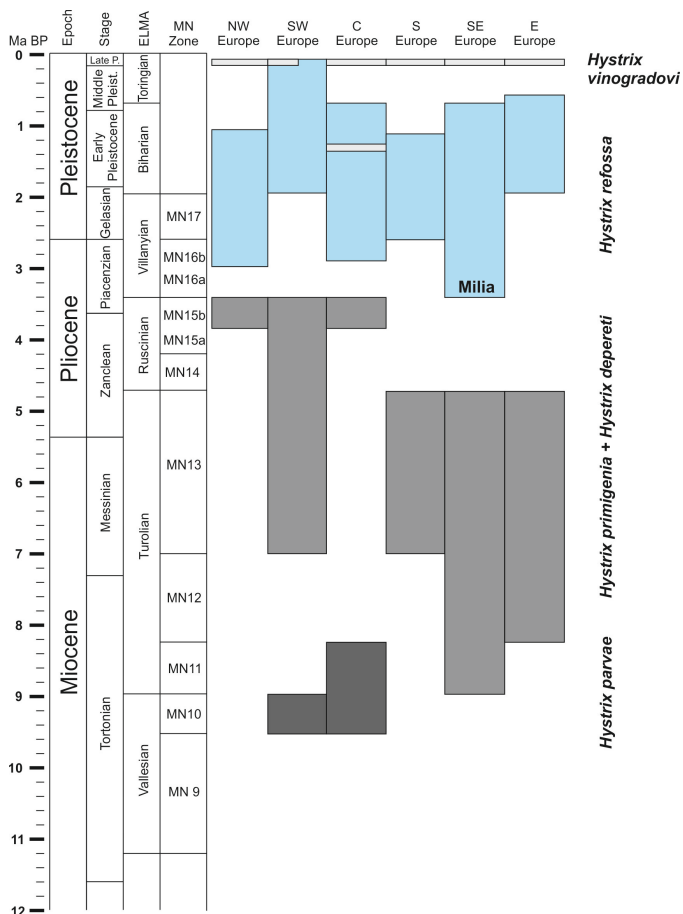


Figure 1 – Stratigraphic range of *Hystrix* species in different regions of Europe. NW Europe – UK, France, The Netherlands; SW Europe – Spain; C Europe – Germany, Poland, Czech Republic, Slovak Republic, Austria, Hungary; S Europe – Italy; SE Europe – Croatia, Serbia, F.Y.R. of Macedonia, Albania, Bulgaria, Greece; E Europe – Romania, Ukraine, Russia. Stratigraphic units and correlation after Hilgen et al. (2012), except Toringian, Biharian and Villanyian, which is after Fejfar et al., 1998.

chyura vinogradovi (Baryshnikov, 2003). The oldest record of this species is from the Early Pleistocene in Hungary (Jánossy, 1972). It became widespread in Europe particularly at the last interglacial/glacial transition (Mottl, 1967; Jánossy, 1964) around 115 ka BP before it disappeared.

Although the history of Hystricidae appears to be grossly clear, details of the stratigraphic (Fig. 1) and geographic ranges, evolutionary relations and of the biogeographic movements are far from resolved. Therefore, any new porcupine records that may improve our knowledge should be reviewed for its significance.

In the Early Villafranchian site of Milia, a single find of *Hystrix* was unearthed among more than 1800 vertebrate remains. Milia is a village of the community of Grevena in northern Greece, with a fossil site well-known for the longest proboscidean tusks in the world (4.39 m and 5.02 m length), of a Borson's mastodon. The fauna comprises the large mammals *Mammuth borsoni* (Hays 1834), *Anancus arvernensis* (Croizet et Jobert, 1828), *Homotherium crenatidens* Fabrini, 1890, *Ursus etruscus* Cuvier, 1823, *Agriotherium* sp., a hipparion of “*Hipparion crassum* Group”, *Tapirus arvernensis arvernensis* Croizet et Jobert, 1828, *Stephanorhinus jeanvireti* (Guérin, 1972), *Sus arvernensis arvernensis* Croizet et Jobert, 1828, *Croizetoceros ramosus* (Croizet et Jobert, 1828), *Praeclaphus* cf. *lyra*, *Alephis* sp., *Gazella borbonica* Depéret, 1884, *Grevenobos antiquus* Crégut-Bonnoure and Tsoukala, 2017, and turtles (Crégut-Bonnoure and Tsoukala, 2017; Tsoukala and Mol, 2016; Vlachos and Tsoukala, 2016; Lazaridis and Tsoukala, 2014; Guérin and Tsoukala, 2013; Tsoukala, 2000). The present paper aims to clarify the taxonomy and significance of the porcupine fossil from Milia.

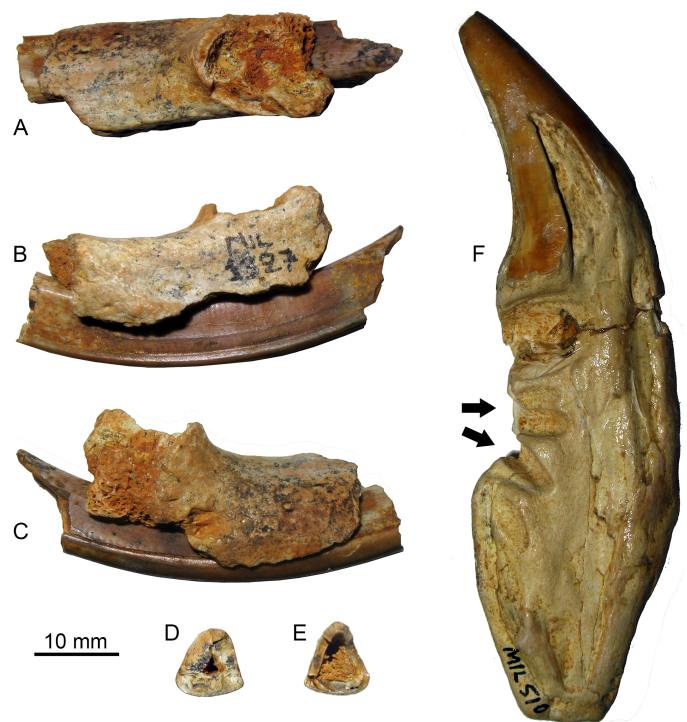


Figure 2 – Milia, *Hystrix refossa*. A-E – Right mandible fragment (MIL1327) with the first incisor fragment; A – occlusal view with the alveolus of the fourth premolar, B – vestibular view, C – lingual view, D – mesial view of incisor cross-section, E – distal oblique view of incisor cross-section; F – left lower canine of *Ursus etruscus* (MIL510) with gnawing marks (see arrows) of *Hystrix*, lingual view. Scale bar 10 mm.

Results

Description

The Milia *Hystrix* find is a right mandible fragment with part of the first lower incisor and the alveolus of the fourth premolar (MIL1327) (Fig. 2A-C). The slightly curved lower incisor has a shape of an equilateral triangle in mesial cross section with the vestibular side being the shortest in the distal view (Fig. 2D, E). Enamel covers the vestibular side completely, more than one-third of the distal (2.9 mm) and a minor part of the mesial side (1.6 mm). This kind of enamel cover on the incisor characterises the genus *Hystrix* (Heller, 1955). The antero-posterior (DAP) and the transversal diameters (DT) are: 7.41 mm and 7.37 mm at the mesial part; and 7.37 mm and 7.31 mm at the distal part of the tooth, respectively.

Variations in the diameter between very young and adult animals were reported by Van Weers and Rook (2003). The Milia specimen obviously belongs to an adult individual, since there is no significant difference in diameter measurements (DAP, DT) between the anterior and posterior end of the incisor. Also on the complete incisor GER-170 of *H. refossa* (originally referred to the junior synonym *H. major* by Koliadimou and Koufos, 1991) from Gerakarou (Mygdonia Basin, Macedonia), we found that the diameters do not change along the tooth length.

Comparison

The identification of fossil porcupine species is based rather on the dimension of the cheek-teeth and their degree of hypsodonty than on the occlusal morphology, since this is quite conservative and displays significant intraspecific variability (Van Weers and Rook, 2003). However, also the size of the incisor is of importance. Two species of Hystricidae were erected based on incisor size: *H. primigenia* (Wagner, 1848) from Pikermi, Greece — based on a left incisor fragment IPGM ASI146 and *Atherurus karnuliensis* Lydekker, 1886, from Cathedral Cave, India — based on a right upper incisor GSIC no. E221a (Van Weers, 2002).

The Milia incisor is compared with those of *Hystrix primigenia*, *H. depereti*, and *H. refossa* from Europe and *H. aryanensis*, *H. paukensis*,

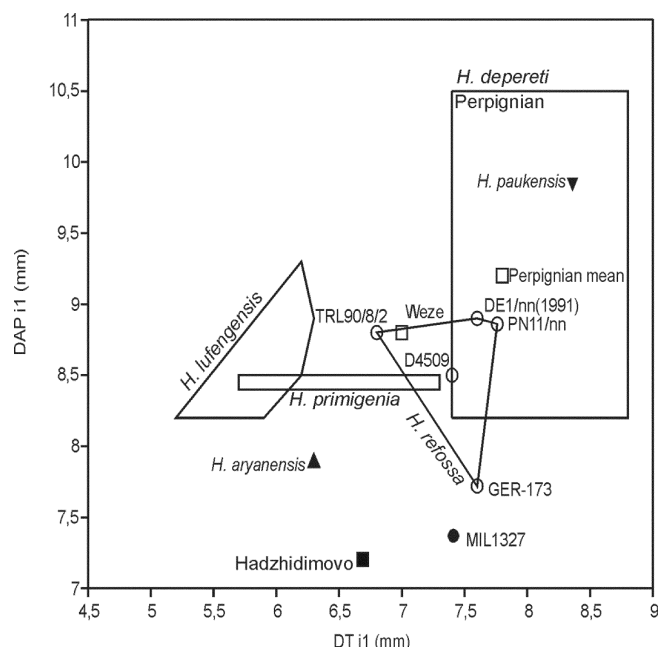


Figure 3 – Lower incisor transversal diameter (DT) vs antero-posterior diameter (DAP) of *Hystrix primigenia* (rectangle and solid square) from Pikermi, Greece (Van Weers and Rook, 2003; Sulimski, 1960), Shahinova, Albania (Fistani et al., 1997) and Hadzhidimovoo, Bulgaria (Kovachev, 2012); *H. depereti* (rectangle and open square) from Perpignan, France (Sen, 2001b) and Weże, Poland (Sulimski, 1960); *H. aryanensis* (triangle) from Iran (Sen and Purabrishemi, 2010); *H. lufengensis* from Lufeng, China (Wang and Qi, 2005); *H. paukensis* from Chaingzauk area, Myanmar (Nishioka et al., 2011); *Milia H. refossa* MIL1327 (solid circle) and *H. refossa* (open circle) from Dmanisi, Georgia (D4509, Vekua et al., 2010); Pirro Nord, Italy (DEI/nn1991), PNII/nn, measurements taken from photos in Rook and Sardella, 2005); Gerakarou, Greece (GER-173) and *H. cf. refossa* from Trlica, Montenegro (TRL90/8/2, Bogičević and Nenadić, 2008).

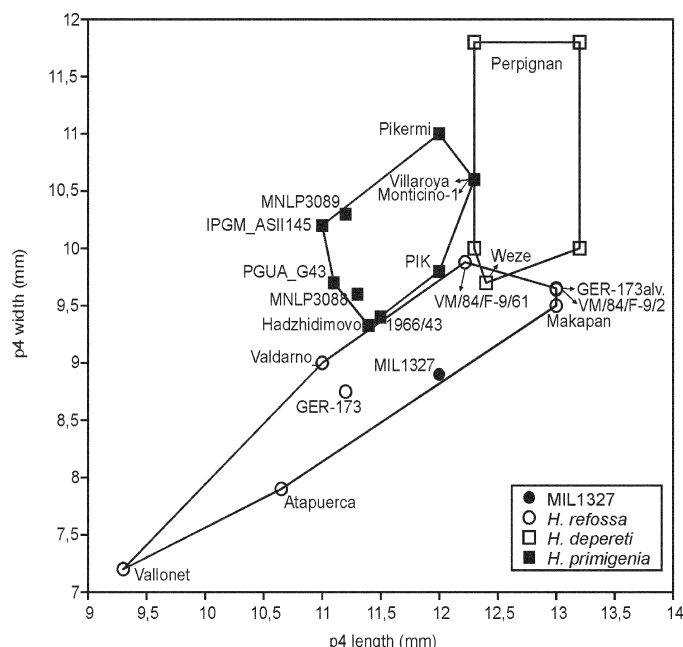


Figure 4 – Width vs length of p4 of *Hystrix primigenia* (solid square) from Pikermi, Greece (IPGM SII45, MNLP3089, MNLP3088, PCGUA G43, Van Weers and Rook, 2003), Pat. Inst. Wien, Mientelsen, 1968, PIK, Sulimski, 1960), Villaroya, Spain (Agusti et al., 1987), Monticino-I, Italy and Hadzhidimovo, Bulgaria (Kovachev, 2012), *Hystrix depereti* (open square) from Perpiñan, France (Sen, 2001b) and Węże, Poland (Sulimski, 1960), *Hystrix refossa* (open circle) from Venta Micena, Spain (VM/84/F-9/61, VM/84/F-9/2), Atapuerca, Spain (Agusti et al., 1987); Makapan, South Africa (Sulimski, 1960), Upper Valdarno, Italy (Bosco, 1898); Vallonnet, France (Chaline, 1972), and Gerakour, Greece (GER-173, Kolaidimou and Koufos, 1991). Specimens GEM-3734v and MIL1327 (solid circle) are alveolus sizes.

and *H. lufengensis* from Asia. The measurements of *H. aryanensis*, *H. paukensis*, and *H. lufengensis* all fall outside the size of MIL1327 (Fig. 3). The DT of the Milia specimen is in the range of and mostly resembles to other *H. refossa* specimens, but the DAP is lower. It is nearly as small as in the specimen of *H. primigenia* from Hadzhidimovo, which, however, seems to be extremely small in comparison to other *H. primigenia* (Fig. 3). The ratio DT/DAP is 99.5% for MIL1327, 98.4% for Gerakarou, 86.5% for Pirro Nord, 77.3% for Trilca and 87.1% for Dmanisi. The *Hystrix* incisors from Milia and Gerakarou in northern Greece have rather similar proportions. The similarity of this ratio implies that this measurement remains stable in the same region through time. In any case, good statistical samples would be required to investigate such pattern. The size (length x width) of the alveolus of p4 from MIL1327 are 12 mm x 8.9 mm. For the Gerakarou specimen (cf. Koliadimou and Koufos, 1991) we measured the respective alveolar dimensions: 13 mm x 9.5 mm, which correspond to 11.3 mm x 8.82 mm of the occlusal size and 12.6 mm x 9.63 mm of the maximum size of the tooth.

In a scatter diagram we plotted p4 width vs length of *H. primigenia*, *H. depereti* and *H. refossa*. The values are quite well separated with only little overlaps (Fig. 4). The length of p4 in *H. primigenia* is smaller than that of *H. depereti*, the width of both species is rather similar. The *Hystrix refossa* length overlaps with both latter species, but the width is generally smaller than in *H. primigenia* and *H. depereti*. However, the largest specimens of *H. refossa* are similarly wide as those of *H. primigenia* and *H. depereti*.

The Milia alveolar measurement falls very well in the range of *H. refossa*, given the similar relation of the tooth and alveolus dimensions, comparable to that of the Gerakarou specimen. The p4 of the other Pleistocene species, *H. (A.) brachyura* and resp. *H. vinogradovi*, are significantly smaller than the Milia specimen.

Porcupines often gnaw on bones and leave typical traces (Kurtén, 1968). The presence of *Hystrix* in Milia is also witnessed on the root of a lower canine of *Ursus etruscus* (MIL510) bearing typical gnawing marks (Fig. 2F). These marks are oriented radically below the cervix at the disto-lingual surface of the tooth.

Summarising the comparison, we refer our specimen to *H. refossa* because of its metrical resemblance with that species and despite its poor preservation. We can exclude by size, the main diagnostic feature, the larger *Hystrix primigenia* and *H. depereti*. There is no reason to express uncertainty in identification and using “cf.” (confer) in our taxonomic referral, since there is no indication that in Europe another species of that size and in this period occurred.

Discussion

The oldest records which had been assigned to *Hystrix refossa* so far, are from Les Etouaires (Perrier) in France (as *H. refossa*) (Van Weers, 1994; Chaline, 1972; Gervais, 1852) and from Osztramos 7 in Hungary (as *H. cf. major*) (Jánossy, 1973). Both faunas yield *M. polonicus* and therefore they have to be placed in the informal Mammal Sub-Zone MN 16b.

The Greek fauna of Damatria produced *Equus* sp., *Sus strozzii*, *Leptobos* sp., *Apodemus* cf. *dominans*, *Thallomys* sp., *Myomimus* sp., *Hystrix* sp., and *Mimomys* cf. *hajnickensis* (Koufos, 2001; Van der Meulen and Van Kolfshoten, 1986; Benda et al., 1977). *Mimomys hajnickensis* is the phylogenetic ancestor of *M. polonicus*, characterised by a somewhat lower linea sinuosa on the molars. Because of this key fossil it is not possible to refer the fauna to MN 16b (Koufos et al., 2005) or even to the MN16/MN17 transition (Koufos, 2016), Damatria has to be placed to the *M. hajnickensis* Sub-Zone MN 16a (the absolute age of which is considered 3.2–2.558 Ma http://fossilworks.org/bridge.pl?a=viewTimeScale&scale_no=109).

In any case Damatria is younger than Milia where *Equus* is lacking but *Hipparion* is still present (Lazaridis and Tsoukala, 2014). The LAD of *Hipparion crassum* is considered to be in MN 15 (Forstén, 2002). Previously, Crégut-Bonnoure and Tsoukala (2017), referred Milia to the earliest part of MN 16, close to the transition MN 15 to MN 16, since *Mammuth borsoni* and the genera *Agriotherium* and *Praeaelaphus* have their last appearance in subzone MN 16a. This age is confirmed by the presence of *Stephanorhinus jeanvireti*, which has also been re-

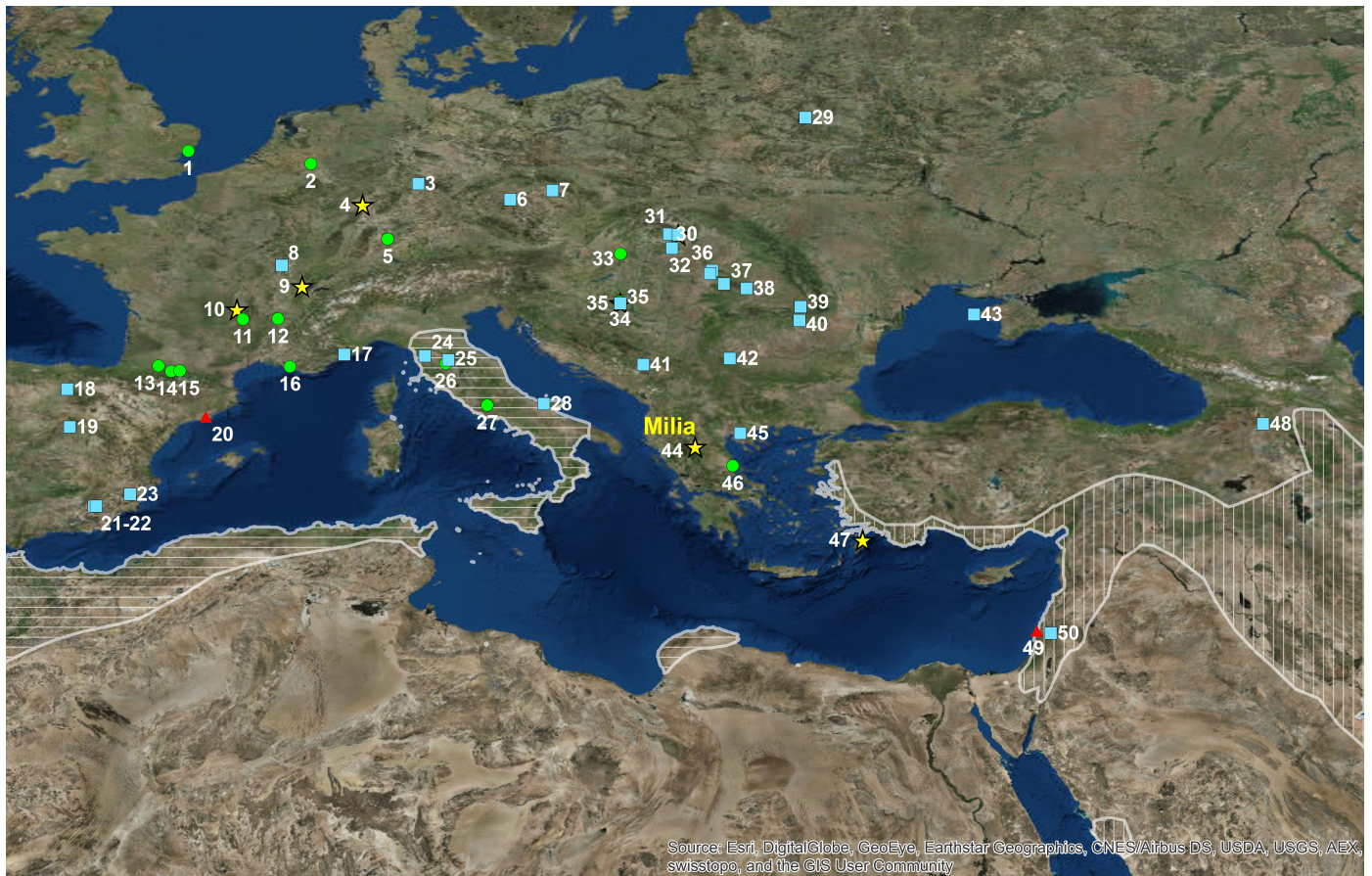


Figure 5 – Records of *Hystrix refoffa* in Europe and in the Near East. Ages: MN 16 – yellow star; MN 17 – green circle; pre-Elsterian Pleistocene – blue square; Late Pleistocene – red triangle. The numbers of localities correspond with the numbers in table 1. UK: 1 – Red Crag; The Netherlands: 2 – Tegelen; Germany: 3 – Untermaßfeld; 4 – Gundersheim 1 and 2; 5 – Erpfinger Cave (Erpfingen 2); Czech Republic: 6 – Koněprusy C 718; 7 – Chlum 4; France: 8 – Fissures des Perrières à Dijon; 9 – Le Coupet; 10 – Les Etouaires (Perrier); 11 – Chilhac; 12 – St. Vallier; 13 – Aurensan; 14 – Montréjeau; 15 – Montsaunès; 16 – Ratonneau; 17 – Vallonnet; Spain: 18 – Atapuerca TD 3-4, 6a, 6b; 19 – Pontón de la Oliva; 20 – Castelldefels; 21 – Fuente Nueva 2; 22 – Venta Micena 2; 23 – Sierra del Quibas; Italy: 24 – Casa Sgherri; 25 – Upper Valdarno faunas of Tasso Faunal Unit; 26 – Upper Valdarno faunas of Olivola Faunal Unit; 27 – Coste San Giacomo; 28 – Pirro Nord PN5, PNII, GP361; Belarus: 29 – Korchova (= Korchevo); Slovak Republic: 30 – Gombasek 1, Gombasek 2; Hungary: 31 – Osztramos 7; Osztramos 8; 32 – Hajnóczy; 33 – Süttő-Dunaalmás; 34 – Villány 3; 35 – Beremend 4 and 16; Romania: 36 – Betsia II (incl. Püspökföld) and Betsia VII/3; 37 – Chişcău 1 Pesteria Ursilor; 38 – Subpiatra; 39 – Brasov; 40 – Valea Grăunceanului; Montenegro: 41 – Trlica; Bulgaria: 42 – Kozarnika B1 and B2; Ukraine: 43 – Tarkhankut; Greece: 44 – Milia; 45 – Gerakarou I; 46 – Volos-Halykés; 47 – Damatria; Georgia: 48 – Dmanisi; Israel: 49 – Geula Cave; 50 – Ubeidiya. Range of extant *Hystrix cristata* (hatched horizontally) (Amori and Smet, 2016), and *H. indica* (hatched vertically) (Amori and Smet, 2016). (This map was created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright ©Esri. All rights reserved. For more information about Esri® software, please visit www.esri.com).

recorded in Viallette in France with an age of 3.14 Ma (Lacombat et al., 2008) that is within MN 16a. The new member of Bovini, *Grevenobos antiquus*, is characterized by a mixture of primitive and advanced morphological features. Its appearance precedes that of *Leptobos*. The particularity of the Milia fauna is the mixture of MN 15 and MN 16a species. Nevertheless, the majority of the newcomer species involved in defining MN 16a are missing. Hence, we propose to attribute this faunal assemblage close to the transition between MN 15 and MN 16a. It is a new European Pliocene assemblage. This fauna marks the first appearance of *Alephis* and *Praeclaphus* in Greece. Milia may be considered as an exceptional locality that has preserved the evidence of the transition between the Ruscinian and Early Villafranchian (Crégut-Bonnoure and Tsoukala, 2017).

We can therefore conclude that the *Hystrix* find from Milia has to be placed into the early part of MN 16a close to the transition between MN 15/MN 16. Since other records of *H. refoffa* are all younger than MN 16a, the recent find from Milia provides so far the oldest record of this species.

In order to see changes in the geographic range within Europe and the Near East through time, we plotted all records currently referred to *H. refoffa* in Fig. 5. References, and original taxonomy of the records are given in Tab. 1. The records are grouped in time intervals of MN 16, MN 17 (Gelasian), pre-Elsterian, and Late Pleistocene.

H. refoffa became extinct during the early Middle Pleistocene, possibly except for Spain, where it is recorded at Castelldefels (*H. major*) (Villalta and Crusafont, 1950) and for Israel, where it occurs in Geula

Cave (Van Weers, 1994; Frenkel, 1970), both Late Pleistocene localities.

Except in Milia, *Hystrix* is not recorded in other localities, well dated to MN 16a, as Hajnačka in Slovakia, Moreda, Zujar, Escorihuela A, and Galera 2 in Spain, Commenailles, Seynes, and Viallette in France and San Giusto, and Arondelli-Tiversa in Italy. Thus, Milia records the earliest colonisation of Europe by *H. refoffa*, beginning from the southern-most edge of the distribution range in Europe. The same is obviously true for *H. primigenia* and *H. depereti*, which also had its oldest European records in the Balkan Peninsula and Anatolia, in contrast to *H. parvae*, whose first occurrences are well known in Central Europe (Fig. 1). Possibly *H. refoffa* and *H. primigenia* had their ancestors in Asia Minor, before arriving in south-east Europe. Scarce findings of *H. primigenia* and *H. depereti* from Late Miocene of Anatolia may support this assumption (Yavuz et al., 2017). Another hint for a starting point of a *Hystrix* expansion in south-eastern Europe could be that the extant *H. indica* has its north-westernmost occurrence in Anatolia (Fig. 5) and possibly would spread to southern Europe if it could cross the Bosphorus.

Obviously, there is no alternative to a dispersal of *Hystrix refoffa* from Anatolia. A derivation from the European *H. depereti*, which had its last appearance in MN 15, is not possible because of data given by Van Weers (1994) on hypsodonty and size of molars: *H. refoffa* from Les Etouaires (MN 16b), one of the oldest known representatives of this species, is smaller and much more hypsodont compared to the stratigraphically youngest *H. depereti* from Perpignan (MN 15). This discontinuity is supported by the fact, that there is no record of *Hystrix*

Table 1 – Records of *Hystrix refossa* remains with original taxonomic assignment and references. The consecutive numbers on the left column are in accordance with Fig. 5.

No.	Country	Locality	Original taxomic assignment
1	UK	Red Crag	<i>H. sp.</i> (McWilliams, 1970; Spencer, 1966)
2	The Netherlands	Tegelen	<i>H. refossa</i> (Van Weers, 1994), <i>H. cf. etrusca</i> (Bernsen, 1932)
3	Germany	Untermaßfeld	<i>H. sp.</i> (Maul, 2001)
4	Germany	Gundersheim 1 and 2	<i>H. sp.</i> (Storch and Fejfar, 1990; Heller, 1936)
5	Germany	Erpfinger Cave (= Erpfingen 2)	<i>cf. H. refossa</i> (Rathgeber, 2003; Lehmann, 1957), <i>H. sp.</i> (Lehmann, 1953)
6	Czech Republic	Koněprusy C 718	<i>H. aff. cristata</i> (Fejfar, 1961, 1956)
7	Czech Republic	Chlum 4	<i>H. sp.</i> (Fejfar, 1963)
8	France	Fissures des Perrières à Dijon	<i>H. major</i> (Chaline, 1972)
9	France	Le Coupet	<i>H. major</i> (Chaline, 1972), <i>Oreomys elaveris</i> (Aymard, 1854)
10	France	Les Etouaires (Perrier)	<i>H. refossa</i> (Gervais, 1852; Van Weers, 1994)
11	France	Chilhac	<i>H. sp.</i> (Guth, 1982)
12	France	St. Vallier	<i>H. refossa</i> (Van Weers, 1994; Viret, 1954)
13	France	Aurensan	<i>Hystrix</i> size of <i>H. major</i> (Chaline, 1972; Harlé, 1910)
14	France	Montréjeau	<i>Hystrix</i> size of <i>H. major</i> (Chaline, 1972; Harlé, 1910)
15	France	Montsaunès	<i>Hystrix</i> size of <i>H. major</i> (Chaline, 1972; Harlé, 1898)
16	France	Ratonneau	<i>H. refossa</i> (Van Weers, 1994), <i>H. major</i> (Gervais, 1859)
17	France	Vallonnet	<i>H. cf. major</i> (Paunesco, 2002; Chaline, 1972)
18	Spain	Atapuerca TD 3–4, 6a, 6b	<i>H. refossa</i> (Cuenca-Bescós et al., 2010)
19	Spain	Pontón de la Oliva	<i>H. cf. major</i> (Sesé and Ruiz Bustos, 1992)
20	Spain	Castelldefels	<i>H. major</i> (Villalta and Crusafont, 1950)
21	Spain	Fuente Nueva 2	<i>H. major</i> (Agustí et al., 1987)
22	Spain	Venta Micena 2	<i>H. major</i> (Agustí et al., 1987)
23	Spain	Sierra del Quibas	<i>H. refossa</i> (Montoya et al., 1999)
24	Italy	Casa Sgherri	<i>H. refossa</i> (Salari and Sardella, 2011; Marcolini et al., 2000)
25	Italy	Upper Valdarno faunas of Tasso Faunal Unit	<i>H. refossa</i> (Azzaroli, 1998; Torre et al., 1996; Rook and Kotsakis, 1994; Masini and Rook, 1993), <i>H. etrusca</i> (Bosco, 1898)
26	Italy	Upper Valdarno faunas of Olivola Faunal Unit	<i>H. refossa</i> (Azzaroli, 1998; Torre et al., 1996), <i>H. etrusca</i> (Bosco, 1898)
27	Italy	Coste San Giacomo	<i>H. cf. refossa</i> (Bellucci et al., 2012; Salari and Sardella, 2011)
28	Italy	Pirro Nord PN5, PN11, GP361, loc. 5, 7, 10, 11, 12, 19	<i>H. refossa</i> (Rook and Sardella, 2013; Van Weers, 1994; Masini and Rook, 1993)
29	Belarus	Korchova (= Korchevo)	<i>H. sp.</i> (Motuzko, 1984)
30	Slovak Republic	Gombasek 1, Gombasek 2	<i>H. sp.</i> (Fejfar, 1961; Kretzoi, 1938)
31	Hungary	Osztramos 7	<i>H. cf. major</i> (Jánossy, 1973)
31	Hungary	Osztramos 8	<i>H. refossa</i> (Van Weers, 1994), <i>H. major</i> (Jánossy, 1972)
32	Hungary	Hajnoczy	<i>H. sp.</i> (Hír, 1985)
33	Hungary	Süttő-Dunaalmás	<i>H. sp.</i> (Jánossy and Krollopp, 1981; Jánossy, 1972; Kormos, 1937, 1925)
34	Hungary	Villány 3	<i>H. sp.</i> (Kretzoi, 1956)
35	Hungary	Beremend 4 and 16	<i>H. sp.</i> (Jánossy, 1996; Kretzoi, 1956)
36	Romania	Betfia II (incl. Püspökfürdő)	<i>H. sp.</i> (Jánossy, 1972; Kormos, 1937)
36	Romania	Betfia VII/3	<i>H. sp.</i> (Terzea, 1994)
37	Romania	Chișcău 1 Pesteria Ursilor	<i>H. sp.</i> (Terzea, 1983)
38	Romania	Subpiatra	<i>H. sp.</i> (Hír and Vencel, 1992, 1991)
39	Romania	Brasov	<i>H. sp.</i> (Jánossy, 1972; Ehik, 1913)
40	Romania	Valea Grăunceanului	<i>H. refossa</i> (Radulesco and Samson, 1990)
41	Montenegro	Trlica	<i>H. cf. refossa</i> (Bogičević and Nenadić, 2008)
42	Bulgaria	Kozarnika B1 and B2	<i>H. refossa</i> (Popov and Marinska, 2007)
43	Ukraine	Tarkhankut	<i>H. sp.</i> (Topachevskij, 1973)
44	Greece	Milia	<i>H. refossa</i> (this paper)
45	Greece	Gerakarou I	<i>H. refossa</i> (Koliadimou and Koufos, 1991)
46	Greece	Volos-Halykés	<i>H. refossa</i> (Athanasios, 2002)
47	Greece	Damatria	<i>H. sp.</i> (Van der Meulen and Van Kolfshoten, 1986; Benda et al., 1977)
48	Georgia	Dmanisi	<i>H. refossa</i> (Vekua et al., 2010)
49	Israel	Geula Cave	<i>H. refossa</i> (Van Weers, 1994), <i>H. angressi</i> (Frenkel, 1970)
50	Israel	Ubeidiya	<i>H. indica</i> (Tchernov, 1996, 1986)

in MN 16a in areas, such as Poland, France, or Spain, which were inhabited by *H. depereti* during MN 15.

Palaeoecological inferences of the *Hystrix* find from Milia can be drawn from their extant relatives. Recent porcupines are strictly nocturnal animals and spend the day in self-dug burrows or those that were created by other animals (e.g., *H. cristata* - Santini, 1980). Sometimes also natural shelters, such as caves, are used as dens. Porcupines live in various landscapes including open and forested habitats but commonly prefer hilly ones and dig burrows close to river banks covered by vegetation. (e.g. Santini, 1980; Kurtén, 1968). Natural shelters were obvi-

ously absent in the surroundings of Milia during the time of the fossil accumulation, as there are no rocky areas today. Therefore, sloping ground is suggested in the case of Milia, as it is commonly preferred for the burrow construction of extant hystricids. The “cross bedded” sand deposits at this site prove the existence of a river running through the area (Lazaridis and Tsoukala, 2014). Vegetated river bank with sloping ground could have been a well suited habitat of porcupines.

Judging from the geographic distribution of extant Hystricidae, members of this family are considered to inhabit warm temperate to hot climates. This seems to hold true also for fossil *Hystrix* species (Hem-

mer et al., 2011). However, Salari and Sardella (2009) compiled information of fossil sites containing the Late Pleistocene *H. vinogradovi* and concluded that an ecology with a wider climatic range was common, which means temperate conditions would be not obligate for this species. We think this is one of the particularities of this Late Pleistocene species, and cannot generalised to all fossil *Hystrix*.

In summary, the palaeoenvironmental conditions for *Hystrix* in the vicinity of Milia consisted of warm and humid climate, with a mosaic of woodland (indicated by *Tapirus*, *Sus* and *Stephanorhinus jeanvireti*) (Guérin and Tsoukala, 2013), and open landscape (indicated by *Gazella* and *Hipparion*), which is also in agreement with palaeoecological requirements of extant porcupines. The temperature decrease was still in its early stages and the opening of the landscape was not dominant (Crégut-Bonnoure and Tsoukala, 2017).

Conclusion

Although the porcupine mandible with the first lower incisor from Milia is fragmented, comparison with other species from various Eurasian localities allows its attribution to *Hystrix refossa*. Until now a gap in the *Hystrsaggiatarrubiaix* records from Greece existed during the Pliocene MN 14–16 zones. The new remain from Milia fills this gap. Compared to all known *H. refossa* records from Europe and the Near East, the age of the Milia fauna (earliest part of MN 16a) provides the first appearance date of this species. The implied habitat of the Milia porcupine is a vegetated river bank within a rough and forested terrain under warm and humid conditions. This fits well with the palaeoenvironmental conditions assumed for the associated fossil fauna.

Of course, a larger sample of *Hystrix* finds including teeth would be desirable. However, until now no small mammal remains could be recorded from Milia sands yet. In terms of biochronology, MN 16a is defined by the presence of the vole *Mimomys hajackensis* (= *M. hassiacus*) (Fejfar et al., 1998). If micro-vertebrate remains will be available from this site in the future, this species would be expected to be present in the small mammal assemblage. Further evidence of *H. refossa* will be required from Pliocene sites in Turkey to clarify the ancestry and the palaeobiogeographic dispersal route of this species. ☞

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