Turolian and Ruscinian porcupines (genus *Hystrix*, Rodentia) from Europe, Asia and North Africa

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with 8 figures and 9 tables

Abstract: Specimens of the larger Neogene porcupines, generally allocated to *Hystrix primigenia* (Wagner, 1848), from 17 localities are studied, and their taxonomic status is reconsidered. Material from one of these localities has recently been described as *Hystrix depereti* Sen, 2001. The diagnoses of both species are revised. Tooth size and crown height are considered diagnostic characters at the species level. As a result, specimens from eight localities are allocated to *H. primigenia*, from eight other localities to *H. depereti*, and from one locality to *Hystrix* sp. indet. The level of specialisation of the cranial morphology of these fossil species is compared with *H. refossa* Gervais, 1852 and with extant species. Diagnostic characters of *H. aryanensis* Sen, 2001 and of *H. zhengi* van Weers & Zhang, 1999, are discussed.

Keywords: Taxonomy, Neogene, *Hystrix primigenia*, *H. depereti*, Europe, North Africa, Asia

Introduction

The oldest porcupines known are from the latest Vallesian (MN 10) and Early Turolian (MN 11) of Europe. These relatively small porcupines were allocated to *Hystrix parvae* (Kretzoi, 1951) by van Weers & Montoya (1996). Discoveries of larger European Neogene porcupines, among which material from Perpignan, have thus far been allocated to *Hystrix primigenia* (Wagner, 1848). Stratigraphically these finds range from the Early-Middle Turolian transition (MN11/12) to the Late Ruscinian (MN15). Finds of European hystricids are rare, so species identifications are generally based on very limited material. The morphological homogeneity of the few skulls from different localities cannot be established with certainty because of their poor preservation. Therefore morphological and phylogenetic implications are based mainly on teeth material.

The occlusal pattern of the cheek teeth within the Hystricidae is notoriously conservative, but shows a large intraspecific variation. The sequence in which the various enamel folds disappear by wear differs considerably. Moreover, the folds are transformed into a variable number of islets, and the homology of the islets and folds cannot always be reconstructed. This circumstance, in combination with small sample size, limits the use of occlusal morphology to distinguish taxa. In most studies, the height of the cheek teeth is indicated with subjective terms only and without indication to the stage of wear. Van Weers & Montoya (1996), for instance, considered *H. primigenia* and the less specialised porcupines *Trichys* Günther and *Atherurus* F. Cuvier as equally "brachyodont". Sen (1999) considered *H. primigenia* "moderately hypsodont", and Sulimski (1960) described the finds from Węże, Poland, allocated to *H. primigenia*, as "highly hypsodont". The subjectivity of these adjectives illustrates that this terminology is inadequate and misleading. In order to avoid this problem, the crown height of all the specimens discussed here will be expressed as a percentage of the tooth length with an indication as to their stage of wear. In the former concept of *H. primigenia*, the maximum enamel height of the cheek teeth measures up to about 150 % of the tooth length, whereas this value may reach 250 % in the M1/2 of *H. refossa* and *H. brachyura*, and 220 % in the m1/2 of these species (van Weers & Montoya (1996). There is indeed a clear break in tooth height between the "brachyodont" older species (*H. parvae, H. primigenia* s.l.) and the younger "hypsodont" ones (Plio-Pleistocene *H. refossa*, extant *H. cristata* and *H. brachyura*). However, Masini & Rook (1993) observed that there are differences between *H. primigenia* from the type locality Pikermi (MN 12) and the remains from Perpignan (France) and Węże (Poland, MN 15). These authors mentioned in the material from Perpignan slightly more hypsodont teeth and somewhat stronger incisors that they attributed to *Hystrix* cf. *primigenia*. This collection from Perpignan has recently been described by Sen (2001a) under the name *H. depereti*. The relatively large number of specimens from Pikermi and Perpignan allow statistical comparison of tooth size and crown height.

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On the base of the data of the new studies, the diagnoses of *H. primigenia*, *H. depereti*, *H. aryanensis* and *H. zhengi* are revised, the taxonomic allocation of the different assemblages is established, the geographical ranges of *H. primigenia* and *H. depereti* are indicated, and the skull morphology is compared among species of the genus.

Material and methods

Measurements and observations

Measurements by Vernier callipers follow VAN WEERS (1976, 1978). The incompleteness and deformation of the fossil skulls lead to inaccuracies in the measurements and hence in the indices derived from these. Therefore, length of the nasals and the height of the skull are expressed, not only as a percentage of the occipito-nasal length, but also as a percentage of the correlated basilar length of the skull.

STEHLIN & SCHAUB (1951) applied a nomenclature for the dental structures of the Hystricidae based on the homologies with their *Theridomys-Trechomys*-plan. BOSMA (1968) and SEN (2001a), among others, followed STEHLIN & SCHAUB's terminology for the occlusal morphology of *Hystrix* teeth based on that nomenclature in which about forty terms may be used. This terminlogy has significance for the comparison of the Hystricidae with other rodent families, but is of no use for the comparison of specimens at the species level within the genus *Hystrix*. Therefore, this study is not aimed at a detailed description of the occlusal morphology with this inappropiate terminology, but rather at a broad comparison of patterns in relation to the classes of wear described by VAN WEERS (1990).

Upper cheek teeth are indicated in upper case, lower ones in lower case. The width (W) and the length (L) of the cheek teeth are the maximum values of the tooth. In unworn teeth, these measurements are larger than when measured at the occlusal surface. When the left and right tooth of a specimen from the same serial position is available, the mean size has been used. The largest enamel height (EH) of upper cheek teeth is measured lingually, buccally on lower cheek teeth. In previous studies (VAN WEERS & MONTOYA 1996; VAN WEERS & ZHANG 1999), the tooth height was expressed in a different way because the enamel/dentine border of some specimens was not visible due to a cover of matrix, tooth cement, or glue. In this study, all types of covering have been removed until the enamel border became visible, and tooth height is the enamel height of the crown. The skulls were X-rayed to establish the position of the cheek teeth in the maxilla before preparing them. The occlusal patterns of the cheek teeth of the various samples are indicated by wear classes of VAN WEERS (1990). For the upper cheek teeth, eight wear classes (A–H) and for the lower teeth six ones (O–T) are given (Tab. 1). These categories are divided into subgroups

Tab. 1. Wear classes and occlusal patterns of the cheek teeth as defined by VAN WEERS (1990) for *Hystrix brachyura*, from unworn (A) to worn down (H) upper teeth, and unworn (O) to worn down (T) lower teeth. *, little or no dentine visible; +, occlusal surface divided into two or more parts. For subnumerals to wear classes see VAN WEERS (1990).

Wear classes		
Upper teeth	Number of folds	Number of islands
A	6 *	0
B	4–6	0
C	3–4	1
D	2–4	2
E	2–3	3
F	1	3–5
G	0	4–6
H	0	0–3
Lower teeth		
O	2–5 *	0–2
P	2–3	0
Q	2–3	1
R	2	2–3
S	1	2–6
T	0	0–6

indicated with a number, but in most cases only the wear class without subgroup number is applied. This classification system does not always fit the lower cheek teeth of fossil specimens because it is based on the extant species *H. brachyura*. The occlusal surfaces of fossil lower teeth often show a larger number of elements in various stages of wear than is observed in extant species. Therefore, occlusal patterns of fossils showing an unusual number of elements are indicated by two letters or are supplemented by a "+".

Institutional abbreviations

AMNH=American Museum of Natural History, New York.
DGAT =Department of Geology and Physical Geography, Aristotele University of Thessaloniki.
DPUA =Department of Paleontology and Historical Geology, University of Athens.
DSTL =Département des Sciences de la Terre, Lyon.
GIN =Geological Institute of Moscow.
GSIC =Geological Survey of India, Calcutta.
HGIB =Hungarian Geological Institute, Budapest.
IPGM =Institut für Paläontologie und Historische Geologie, München.
ISEK =Institute of Systematics and Evolution, Krakov.
MESW=Museum of Earth Sciences, Polish Academy of Sciences, Warsaw.
MMLY=Muséum Municipal de Lyon.

MMPE =Muséum Municipal de Perpignan.

MNLP =Muséum National, Laboratoire de Paléontologie, Paris.

MSNF =Museo Civico di Storia Naturale di Faenza.

MTA =M.T.A. Müdürlügü, Ankara.

Specimens studied

Pikermi, Megalorema, Greece

type locality of *Hystrix primigenia*.

- IPGM, ASII144, skull (WAGNER 1857: pl. 5 fig. 12); ASII145, right mandible fragment with p4 and m1 (ROTH & WAGNER 1854: pl. 10 fig. 3); ASII146, left incisor fragment, holotype of *Lamprodon primigenius* WAGNER, 1848 (: pl. 12 figs. 7 and 8).
- MNLP, Pik.3088, right mandible with p4-m2 (GAUDRY 1862: pl. 18 fig. 12); Pik.3089, right mandible fragment with p4-m3 and incisor (GAUDRY 1862: pl. 18 fig. 4); Pik.3116, right maxillary fragment with P4-M3 (GAUDRY 1862: pl. 18 fig. 3); Pik.3073, right upper incisor; Pik.3191, left upper incisor fragment.
- DPUA, Pik.G.43, left mandible fragment with p4-m3 and incisor; Pik.G.44, left and right mandible with m1-m3.

Dytico, Greece

- DGAT, DKO-41, skull, Dytico-3.

Bayirköy, Turkey

- MTA, without catalogue no., right mandible with p4-m3, (ÜNAY & DE BRUIJN 1984).

Gülpınar, Turkey

- MTA, without catalogue no., right mandible fragment, with p4-m2.

Kemiklitepe, Turkey

- MNLP, KT-1, palate with left and right P4-M3 (SEN 1994: fig. 1); KTA-17, maxilla fragment with M2-M3; KTA-69, right mandible fragment with p4.

Şerefköy, Turkey

- MTA, M-Y, left mandible fragment with p4-m3, Muğla-Yatağan.

Taraklia, Moldavia

- GIN, 1256/3085, skull fragment with right P4-M3 and left M2-M3, holotype of *Hystrix bessarabica* RIABININ, 1929.

Siwaliks, India

- GSIC, D 96, right mandible fragment with m1 and m2, holotype of *H. sivalensis* LYDEKKER, 1878.

Perpignan, France

type locality of *Hystrix depereti*.

- MMPE, coll. A. DONNEZAN from Serrat d'En Vaquer: P.R.24, left mandible with p4-m3 (DEPÉRET 1890: pl. 4 fig. 12); P.R.25, left mandible fragment with p4-m3, holotype of *H. depereti*; P.R.26, P.R.151, upper incisors; P.R.148, P.R.150, lower incisors; P.R.27, P.R.155, right M1/2 (DEPÉRET 1890: figs. 15, 16); P.R.147, left mandible fragment with dp-m2 and part of incisor; P.R.152, left p4; P.R.153, right M1/2; P.R.154, left M1/2; P.R.156, right m3.
- MNLP, four unnumbered upper cheek teeth, right P4, left P4, right M1/2 and left M3.
- MMLY, Pp55, right mandible fragment with p4-m2; Pp58a, right mandible fragment with p4 and damaged m1-m2; Pp58b, 58c, two left m3.
- DSTL, without catalogue no., left m1/2, coll. P. MEIN, F-34 Sète.

Teruel, Spain

- DSTL, without catalogue no., right M1/2, coll. P. MEIN, E-Teruel, Villastar.

Samos, Greece

- AMNH, 20551, skull, quarry 5, coll. B. BROWN, 1923; 23030, left mandible fragment with incisor and part of m3, coll. B. BROWN, 1924.

Çoban Pınar, Turkey

- MTA, eight upper molars without catalogue nos., apparently belonging to one adult.

Węże, Poland

- ISEK, coll. MF/549/61, Weze I: 1A = left m1-m2, 1B = left dp4, 1C = left lower incisor; 2A = right m2, 2B = right m3, 2C = part of alveoli, 2D = sediment fragment with part of incisor; 3 = left M1/2 in sediment fragment; 4 = DP and M1 in sediment fragment, 5 = M3 or M1/2 in sediment fragment.
- MSEW, MZVIII-Vm-731/1, skull fragment with right P4-M1 and left M1-M3 (Rod. 1 in SULIMSKI 1960), and 731/2, right mandible fragment with p4-m2 (Rod. 2 in SULIMSKI 1960).

Brisighella, Italy

- MSNF, BRS Err., left mandible fragment with p4-m3; BRS 29/1, right P4; BRS 29/2, 29/3, right M1/2.

Kalimanci, Bulgaria

- MNLP, casts of the collection from Kalimanci, Bulgaria (SEN & KOVATCHEV 1987), palate with right P4-M3 and left P4-M1, left upper jaw fragment with M1-M3, left mandible fragment with m2-m3.

Menacer, Algeria

- MNLP, Ama1-Ama5 (ARAMBOURG 1959: pl. 5 figs. 11-13, and 1986), 1 = left m1/2, 2 = right M1/2, 3 = right m1/2, 4 = right M1/2, 5 = right P4, Menacer = formerly Marceau.

Polgárdi, Hungary

- *Hystrix* sp. indet. HGIB, Ob.4619 A-F, A = left p4, B = right p4, C = right m1/2, D = right M3, E = right M1/2, F = unworn m1/2 ?

Molayan, Afghanistan

type locality of *Hystrix aryanensis* SEN, 2001.
• MNLP, MOL-51, skull fragment with right DP4-M3 and left DP4-M2, holotype; MOL-52, left maxilla with P4-M2, paratype.

Taxonomy

Reconsideration of the taxonomic status of Neogene species

Order Rodentia BOWDICH, 1821
Family Hystricidae FISCHER, 1817
Subfamily Hystricinae LYON, 1907

Genus *Hystrix* LINNAEUS, 1758
Subgenus *Hystrix* (*Hystrix*) ELLERMAN, 1940

This subgenus comprises the larger *Hystrix* species, with high crowned as well as low crowned cheek teeth, and relatively large nasals and high skulls.

Hystrix (*Hystrix*) *primigenia* (WAGNER, 1848)

* 1848 *Lamprodon primigenius* WAGNER: 374, pl. 12 figs. 7–8.
　1854 *Castor atticus*. – ROTH & WAGNER: 414, pl. 10 fig. 3.
　1856 *Hystrix primigenia*. – GAUDRY & LARTET: 273.
　1857 *Hystrix primigenia* WAGN. – WAGNER: 129, pl. 5 fig. 12.
　1862 *Hystrix primigenia*, GAUD. et LART. (sp. WAGN.). – GAUDRY: 122, pl. 8 figs. 1–12.

1878 *Hystrix sivalensis* LYDEKKER: 100.
1929 *Hystrix bessarabica* RIABININ: 112, pl. 10 figs. 1–1a.

Holotype: Left lower incisor fragment, UPGM ASII146.
Type locality: Pikermi, Megalorema, Greece.
Stratigraphical range: Late Miocene (MN 11–MN 13).
Geographical range: E. Europe (Fig. 1), W. Asia and India (Siwaliks).

Revised diagnosis: Very large porcupine compared with extant species, with enamel height of unworn cheek teeth not exceeding their length.

Differential diagnosis: *Hystrix primigenia* is larger than *H. parvae*, on average larger than *H. cristata*, and slightly larger than *H. refossa*. The length of the cheek teeth of *H. primigenia* is on average slightly smaller than in *Hystrix depereti*. The height of the enamel of unworn cheek teeth is less than the length in *H. primigenia*, in contrast to 150 % of the length in unworn teeth of *H. depereti*. The enamel in cheek teeth of *H. primigenia* is in comparable stages of attrition always lower than in *H. refossa*. The length of the p4 of *H. primigenia* does not differ from *H. zhengi*, but the crown of that tooth of *H. zhengi* is higher.

Hystrix (*Hystrix*) *depereti* SEN, 2001

1890 *Hystrix primigenia* GAUDR. (sp. WAGN.). – DEPÉRET: 43, pl. 7 figs. 12–16.
1959 *Hystrix* sp. – ARAMBOURG: 21, pl. 5 figs. 11–14.
1959 *Hystrix primigenia* GAUDRY & LARTET. – BAKR: 12.
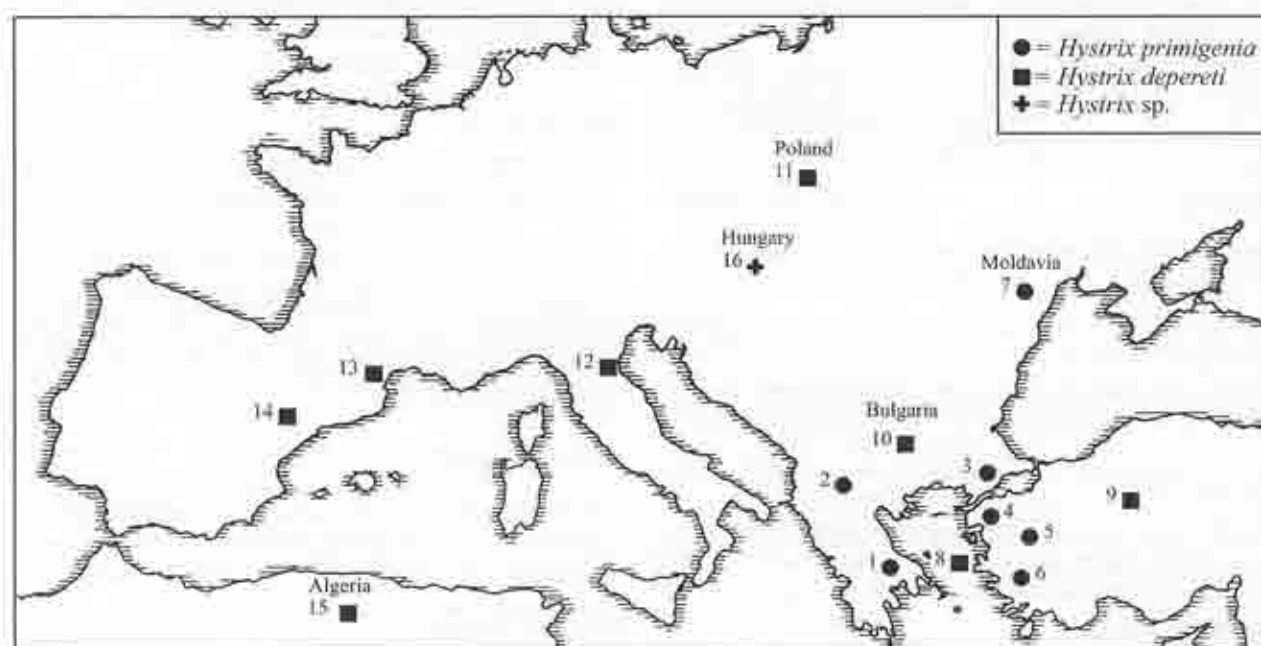1960 *Hystrix primigenia* (WAGNER). – SULIMSKY: 320.

Fig. 1. Localities of *Hystrix primigenia* and *Hystrix depereti* in Europe, Turkey and N. Africa. 1, Pikermi; 2, Dytico; 3, Bayirköy; 4, Gülpınar; 5, Kemiklitepe; 6, Şerefköy (Muğla-Yatağan); 7, Taraklia; 8, Samos; 9, Çoban Pınar; 10, Kalimanci; 11, Węże, 12, Brisighella; 13, Perpignan; 14, Las Casiones; 15, Menacer.

1965 *Hystrix primigenius*. – OZANSOY: 13, tab. 3.
1981 *Hystrix primigenia*. – SOLOUNIAS: 256.
1987 *Hystrix primigenia* (WAGNER), 1848. – SEN & KOVATCHEF: 317, figs. 1–3.
1994 *Hystrix primigenia* (WAGNER, 1848). – SEN: 98, fig. 1, pl. 1 figs. 1–2.
2001a *Hystrix* cf. *primigenia* (WAGNER, 1848). – SEN: 310, fig. 6.
*2001a *Hystrix depereti* SEN: 305, fig. 4A.

Holotype: Right mandible fragment, kept in the Museum of Natural History of Perpignan, France, P.R.25, coll. A. DONNEZAN.
Type locality: Serrat 'den Vaquer near Perpignan, Roussillon, France.
Stratigraphical range: Late Miocene and Pliocene (MN12–MN 15).
Geographical range: Europe (Fig. 1), and N. Africa (Algeria).

Revised diagnosis: Very large porcupine compared with extant species, with the enamel height in unworn cheek teeth larger than the length of the tooth, but not exceeding 150% of the tooth length.

Differential diagnosis: Length of the cheek teeth greater than in *H. parvae*, and on average larger than in *H. primigenia* and *H. refossa*. Height of the enamel crown of unworn cheek teeth of *H. depereti* generally larger than their length (in *H. primigenia* it is smaller than the length). Enamel height of unworn cheek teeth in *H. depereti* not above about 150 % of the tooth length, as opposed to generally above 150 % of the tooth length in *H. refossa*. The p4 of *H. depereti* is longer than in *H. zhengi*, the relative height of the cheek teeth of *H. depereti* is on average less than in *H. zhengi*.

Hystrix (Hystrix) aryanensis SEN, 2001

*2001b *Hystrix aryanensis* SEN: 916, pl. 1 fig. 2.

Holotype: Incomplete skull with basicranium and palate with right dP4-M3 and left dP4-M2, MNHN MOL,-51.
Paratype: Left maxilla with P4-M2, MNHN MOL-52.
Type locality: Molayan, Khurdkabul Basin, Afghanistan.

Revised diagnosis: Size similar to that of *Hystrix cristata*. Upper molars moderately high, enamel height ranging from 108–137 % of the tooth length. The connection between the lingual and the second buccal fold lasts in relatively advanced stages of wear.

Differential diagnosis: The upper tooth rows diverge, but are parallel or convergent in *H. cristata* and *H. indica*. The tooth size is larger than in *H. parvae* but smaller than in *H. primigenia*. The tooth height is larger than in *H. primigenia*, on average larger than in *H. parvae*, the same as in *H. depereti*, and smaller than in the extant species of *Hystrix*. The connection between the lingual and the second buccal fold in upper molars persists to more advanced stages of wear than in other species of *Hystrix*.

Hystrix (Hystrix) zhengi VAN WEERS & ZHANG, 1999

* 1999 *Hystrix zhengi* VAN WEERS & ZHANG: 56, figs. 1A–C.
1987 *Hystrix magna* PEI: 115.
1993 *Hystrix magna* PEI. – ZHENG: 124, fig. 57a.
1998 *Hystrix* sp. – VAN WEERS & ZHENG: 55.

Holotype: Left lower premolar, IVPP V9669.
Type locality: Site of Longgupo, fissure zone 6, Wushan County, Sichuan Province, China.
Geographic range: Apart from the type locality, only known from the Gigantopithecus Cave, Liucheng, Guangxi, China.
Age: Late Pliocene.

Revised diagnosis: Large sized porcupine with height of the lower premolars 90 to 100 % (mean = 96 %, n = 4) of the tooth length.

Differential diagnosis: *Hystrix zhengi* is larger than the extant *Hystrix* species. Its lower premolars are higher than in *H. primigenia* (35–95 %, mean = 68 %, n = 8) and on average higher than in *H. depereti* (72–116 %, mean = 87 %, n = 7). *H. zhengi* differs from *H. depereti* also in shorter length of the p4 , mean 11.7 (range 11.0–12.2 mm, n = 4) compared to the mean of 12.4 mm (range 10.7–13.2 mm, n = 8) in *H. depereti*.

Hystrix (Hystrix) refossa GERVAIS, 1852

*1852 *Hystrix refossa* GERVAIS: 8, pl. 48 fig. 11.
1859 *Hystrix major*. – GERVAIS: 512.
1898 *Hystrix etrusca*. – BOSCO: 142, pl. 1 figs. 1–9.
1970 *Hystrix angressi*. – FRENKEL: 53, pl. 5 fig. 6.

Holotype: Fragment of a right mandible with p4 and four alveoles of the m1 roots, kept in MNLP.
Type locality: Les Etouaires, Perrier, Puy-de-Dôme, France.
Geographic range: Central and southern Europe, Israel.
Age of the type locality: Early–Late Pliocene, Villanyian, MN zone 16.
Stratigraphical range: Early Villanyian to Late Pleistocene.

Revised diagnosis: Very large porcupine compared with extant species, cheek teeth with very high enamel crowns.

Differential diagnosis: About the same size as *H. primigenia* but with much higher molars, enamel height from 150 to 250 % of the tooth length, compared to rarely above 100 % in *H. primigenia*. Molars also higher than in *H. depereti* with molars scarcely above 150 % of the tooth length.

Analysis and allocation of the material studied

Diagnostic characters

Tooth length and width: The length (L) and width (W) of all the individual cheek teeth and the width of the incisors of *H. primigenia* from the type locality Pikermi are given (Tab. 2). Means and ranges for these dimen-

Tab. 2. Measurements of width of upper (I W) and lower (i W) incisors, tooth row length, length (L), width (W), and enamel height (EH) in mm, enamel height in % of length (E/L), and wear class (Cl) of the cheek teeth of *Hystrix primigenia* from the type locality Pikermi, Greece.

Upper teeth	IPGM ASII144	MNLP 3116	Lower teeth	IPGM ASII145	MNLP 3089	MNLP 3088	PGUA G 43	PGUA G 44
I W	7.0		i W		6.7	5.7	6.8	6.3
P4 – M3	39.3	41.0	p4 – m3		39.4		42.1	43.4
P4L	10.8	10.9	p4 L	11.0	11.2	11.3	11.1	
W	11.2	11.0	W	10.2	10.3	9.6	9.7	
EH	10.0	9.9	EH	10.5	8.2	4.6	7.9	
E/L	93	91	E/L	95	73	41	71	
Cl	G4	E	Cl	O	Q+	T2	R+	
M1L	9.0	9.5	m1 L	11.6	9.9	9.0	9.7	10.4
W	10.2	10.6	W	9.2	8.7	8.4	8.8	8.7
EH	6.5	6.8	EH	8.4	6.2	3.5	6.4	
E/L	72	72	E/L	72	63	39	66	
Cl	G4	G4	Cl	Q+	R+	T2	S+	P+
M2L	9.8	10.0	m2 L		11.0	9.6	11.2	10.6
W	10.8	10.6	W		9.3	8.5	9.2	9.4
EH	6.9	8.0	EH		5.4	3.9	5.5	
E/L	70	80	E/L		49	41	49	
Cl	G4	F	Cl		S+	T2	R+	Q
M3L	9.0	9.0	m3 L		9.8		9.4	9.8
W	9.4	9.2	W		8.6		8.7	8.6
EH	6.4	7.4	EH		4.5		5.5	9.5
E/L	71	82	E/L		46		59	97
Cl	D	E	Cl		T2		T2	O1

Tab. 3. Length of tooth series, length (L), width (W) in mm, and relative enamel height (E/L) in % of length with wear class of cheek teeth of samples allocated to *Hystrix primigenia* from a number of localities, with mean, range, and number of specimens (n).

	Pikermi mean(n)range	Dytico n = 1(l+r)	Bayirköy n = 1	Gülpmar n = 1	Kemiklitepe mean(n)range	Şerefköy n = 1	Taraklia n = 1
P4–M3	(2) 39.3–41.0	38.2–39.8			(1) 38.5		38.5
P4L W E/L	(2) 10.8–10.9 11.0–11.2 91(E)–93(G)	11.5 11.8 74 (E/F)			(1) 10.6–11.3 10.2–10.4 93(D)–94(D)		10.1 10.2
M1/2L W E/L	9.6(4) 9.0–10.0 10.8 10.2–10.8 74 70(G)–80(F)	9.1– 9.6 11.2–12.6			9.4 (4) 9.0–9.9 9.9 9.2–11.1 60 42(G)–68(G)		8.7–9.2 9.2–9.4
M3L W E/L	(2) 9.0 9.2–9.4 71(D)–82(E)	8.0–8.2 8.0–8.5			8.4(3) 8.0–9.3 7.5–12.7 80 52(G)–99(E)		9.1 8.2–8.3
p4–m3	41.6(3)39.4–43.4		39.8			41.2	
p4 L W E/L	11.2(4)11.0–11.3 9.9 9.6–10.3 70 (41): R/S)–95(O)		10.7 9.2 64 (Q/R)	11.5 9.8 92 (R)	(1) 12.2 10.8 70(T)	11.2 10.0 35 (T)	
m1/2L W E/L	10.3(9) 9.0–11.6 8.8(9) 8.4–9.4 54(7)39(T)–72(Q)		8.8–9.3 8.2–8.3 50 (S/T)–63 (S)	10.1–11.2 9.0–9.8 55 (R/S)–59 (S)		8.8 – 11.1 9.0 – 10.0 23 (T) – 28 (T)	
m3L W E/L	9.7(3) 9.4–9.8 8.6 8.6–8.7 67 46(T)–97(Q)		9.6 7.6 50 (S)			10.4 9.9 29 (T)	

sions are compared with data for other localities yielding *H. primigenia* (Tab. 3). Similarly means and ranges of the cheek teeth from Perpignan and other localities yielding *H. depereti* are compared (Tab. 4). The teeth from Perpignan in all positions, except the poorly represented M3, are on average larger than those from Pikermi. Statistical comparison between assemblages from different localities with a sufficient sample size is only meaningful with the m1/2 and the p4 from Pikermi and Perpignan. The lengths of the m1/2 (n = 9) from Pikermi (Tabs. 2, 3) are significantly less than those (n = 10) from Perpignan (Tab. 4, Fig. 2). The relatively small width of a tooth from Perpignan in that diagram (8.9 mm) can be considered as individual variation because this tooth is an m1 from the same mandible in which the m2 measures 9.9 mm. A statistical test of the length difference between the p4 (n = 4) from Pikermi and those from Perpignan (n = 5) shows a highly significant difference of the means. The larger length of the Perpignan teeth is also reflected in the length of the p4-m3 series (Tabs. 3, 4).

The largest width of the upper incisors from Pikermi is 7.0 mm (n = 3), against 7.4 mm in the sample of Perpignan (n = 2). For the lower incisors these maximum dimensions are 7.3 mm (n = 5) in Pikermi and 8.3 mm (n = 3) in the Perpignan specimens. Although incisor size depends on age, these maximum dimensions support the conclusion that the Perpignan porcupine is larger than the one from Pikermi.
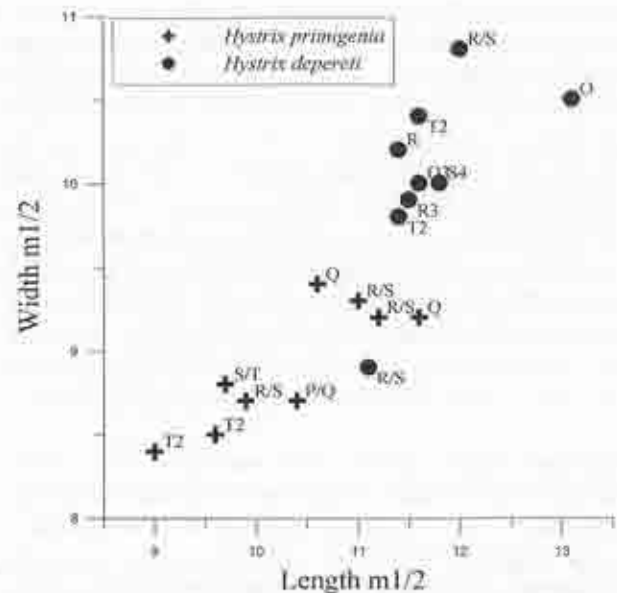

Fig. 2. Diagram of length and width of the m1/2 of *Hystrix primigenia* and *Hystrix depereti* with indication of the class of wear. Scale bars in mm.

Cheek tooth height: The enamel height of the individual cheek teeth from Pikermi is given in mm and as a percentage of tooth length and with wear class (Tabs. 2, 3). The teeth in all positions of Perpignan (Tab. 4) are on average higher, although there is a considerable overlap

Tab. 4. Length of tooth series, length (L), width (W) in mm, and relative enamel height (E/L) in % of the tooth length with wear class of the cheek teeth of samples allocated to *Hystrix depereti* from a number of localities with mean, range and number of specimens. *. Measurements from casts.

	Perpignan mean (n) range	Çoban Pınar n = l (l + r)	Wężé mean (n) range	Brisighella	Kalimanci* mean(n) range	Menacer
P4–M3		40.5	45		(1) 44.1	
P4 L W E/L	(2) 11.2–11.3 9.9–10.3 96 (D)–103 (D)	11.3–11.6 9.5–9.7 86 (C)–96 (C)	(1) 12.5 12.0	(1) 11.0 10.2 132 (B)	(2)11.8–12.2 12.2–12.3	11.2 10.1 116 (B)
M1/2 L W E/L	10.3 (5) 9.6 – 10.8 10.0 8.9 – 10.7 93 93 62 (G)–120 (G)	9.3–10.4 9.3–9.7 81 (D)–107 (D)	10.2 (4) 9.6–10.7 (3) 9.4–10.2 9.9(2)106 (F)–150 (A)	(2) 9.2–10.1 9.1–9.9 121 (C)–125 (D/E)	10.4 (6)10.0–11.2 10.8 (5)10.1–11.8	(2) 9.9–10.6 9.5–10.0 100 (F/G)–103 (C)
M3 L W E/L	(1) 8.7 9.0 121 (E)	9.5–9.7 8.3–8.6 105 (C)–108 (C)	(1) 9.5 9.7		9.4(4) 8.8–10.0 9.2(3) 9.0–9.3	
p4–m3	47.5		47.0	46.9	(1)44.0	
p4 L W E/L	12.9(5) 12.3–13.2 11.0 10.0–11.8 89 89 71 (R)– 16 (O)		(1) 11.9 10.2 86 (Q/R)	(1) 12.3 10.8 76 (R/S)	(1) 10.7 9.3	
m1/2 L W E/L	11.7 (10) 11.1–13.1 9.9 (9) 8.9 – 10.8 78 (9) 53 (T) – 110 (O)		10.8 (5) 10.2–11.6 9.3(5) 8.4–10.2 93 (4) 57 (T)–115 (O)	(2) 10.8–11.0 10.4–10.9 (1) 82 (T)	11.3 (4)10.8–12.0 9.3–10.4	(2) 9.5–11.1 7.6–8.8 70 (Q/R)–87 (O)
m3 L W E/L	10.0 (5) 9.6–10.5 8.7 (5) 8.4–9.0 82 (4) 55 (T)–101 (P)		(1) 10.8 9.3 109 (O)	(1) 10.4 9.4 67 (S)	(2)10.2–10.3 8.3–9.5	

of the ranges. For judgment of these differences, however, the stage of attrition has to be taken into account. The highest M2 from Pikermi (E/L = 80 %, Tab. 2) is not extremely worn (class F), but is much lower than the highest M2 of Perpignan (E/L = 120 %, Tab. 4) which is more worn (class G). This difference in stage of wear makes the size difference more conclusive. The farthest worn m1/2 from Pikermi and Perpignan, both of wear class T, show relative heights of 39 % and 53 %, respectively. The p4 teeth from Perpignan are also higher than those from Pikermi, shown by the scarcely worn p4 from Pikermi (class O) with an E/L of 95 %, compared to 116 % in that of Perpignan at the same class of wear.

Size and shape of the third molars. SEN (2001a) agreed with DEPÉRET (1890) that the third molars of the specimens from Perpignan are reduced in size and almost triangular in occlusal outline compared with *H. primigenia*. However, the relatively smaller size of the third cheek teeth is very common in *Hystrix*. Data in our files show that in *H. brachyura* the length of the M3 varies from 74 % to 95 % of the P4 (mean 84 %, n = 22) and the m3 from 72 % to 100 % of the p4 (mean 83 %, n = 20). Similar ratios are found in *H. indica* (n = 10). In *H. cristata* these differences are smaller with means of 88 % and 94 % (n = 30), respectively. This M3/P4 ratio is 83 % in the two series from Pikermi and 78 % in one from Perpignan. Of two m3 from Pikermi the ratios are 85 % and 87 %, and in two series from Perpignan, 73 % and 78 %. Similar ratios are found in the width of these teeth. Against the background of the variation noted in the genus, smaller size of the third molars of *H. depereti* is far from significant. The occlusal outline of the third molar is highly variable in *Hystrix*, it varies greatly with the stage of attrition, and more or less triangular third molars occur in all *Hystrix* species. Contrary to SEN (2001a: 305), the third molars in *H. depereti* and *H. primigenia* are considered to be very similar.

Material allocated to *Hystrix primigenia*

Pikermi and Dytico (Greece): Skull structure: – Skull UPGM ASII144 (Figs. 3A-B) from the type locality Pikermi, Greece, was mentioned by WAGNER (1857) who figured a tooth series only. This skull was fully described and figured by AZZAROLI (1998). DE BONIS et al. (1992) described and figured an adult skull from Dytico, Greece (AUTG m.DKO-41), which has the same size as the Pikermi specimen. Measurements of both specimens are presented (Tab. 5), together with the dimensions of the two skulls of the Plio-Pleistocene *H. refossa* GERVAIS, 1852 (type material of "*H. etrusca* BOSCO, 1898") and of the extant species *H. brachyura* LINNAEUS, 1758, *H. indica* KERR, 1792, and *H. cristata* LINNAEUS, 1758. The dorsal sutures of the two *H. primigenia* skulls cannot be distinguished, so the length of the nasal bones cannot be measured. BONIS et al. (1992) measured the length of the nasals in the Dytico specimen
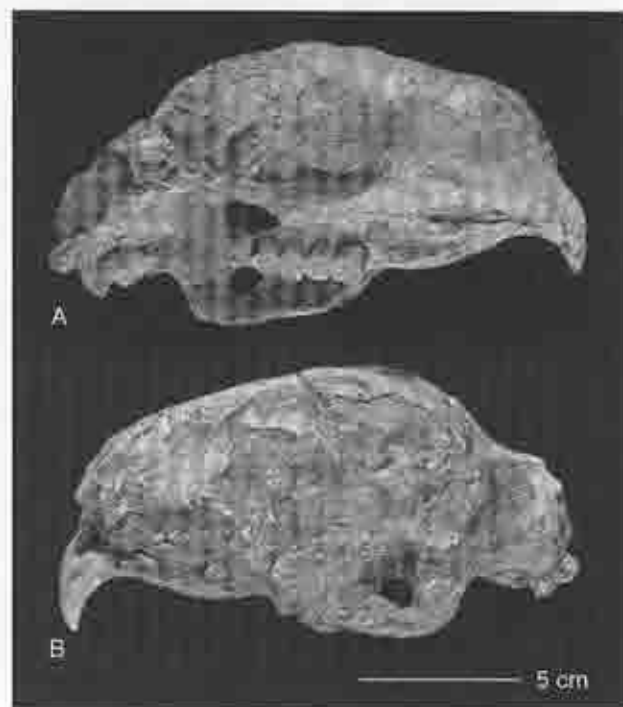

Fig. 3. – **A:** Right-ventral, and **B:** left-upper view of skull IPGM ASII144 of *Hystrix primigenia* from Pikermi, Greece. – Photographs kindly supplied by Dr. K. HEISSIG, München.

"from the alveolus of I1/ to the end of the nasal cavity", but this measurement is very different from the nasal length as measured at the dorsal skull surface. The skull from Dytico seems to be somewhat higher (Tab. 5) than the Pikermi specimen as shown by both relative height indices, but due to the uncertainty in these measurements, the difference is not significant. The height of these two *H. primigenia* skulls is about the same as that of extant *H. (Acanthion) brachyura* and *H. (Hystrix) indica*, but is less than in the Plio-Pleistocene *H. refossa*. The relative height of the *H. refossa* skull is estimated at about 47 % of the occipito-nasal length, based on the 39 % of the dorso-ventrally compressed skull and 55 % of the laterally compressed one (Tab. 5). This height estimate may be between 42 % and 53 % of the basilar length of the skull. The estimates agree with AZZAROLI's (1998: fig. 1) outline of restoration of the "*H. etrusca*" skulls. In regard to this character, *H. refossa* is more specialized than *H. primigenia*.

Tooth dimensions: – The length of the tooth-row (Tab. 3) of the skull from Dytico agrees with that of the sample from Pikermi, as does incisor width of 6.5 mm versus max. 7.0 mm in the Pikermi specimens (n = 3). The moderately worn P4 (Tab. 3) is larger than the two specimens from Pikermi, but may fall within the same (unknown) range. The low enamel height of this P4 (8.5 mm, 74 %) agrees with the Pikermi teeth. The length of the left and right M1 (9.1 and 9.0 mm, class G7) and M2 (9.4 and 9.6 mm, class F and G1) fall within the range of the sample from Pikermi. The large width of the M1 and M2 (12.6 and 11.2 mm, wear class G7 and

Tab. 5. Dimensions in mm with mean, sample size, and indices in % of skull length from Samos (*Hystrix depereti*), Pikermi and Dytico (*Hystrix primigenia*), Plio-Pleistocene *Hystrix refossa* (Italy), and extant *Hystrix brachyura*, *Hystrix indica*, and *Hystrix cristata*. — Occ.n.l., occipito-nasal length; Bar.l., basilar length; Na.l., nasal length; Na.w., width of the nasals; Zyg.w., zygomatic width; Ht., height of the skull. Numbers with * are estimated values, ** indicate specimen numbers from CORBET & JONES (1965). For dimensions between brackets see text.

	Neogene species			Plio-Pleist. sp.		Extant species		
	H. dep.	*H. primigenia*		*H. refossa*		*H. brachyura*	*H. indica*	*H. cristata*
	Samos	Pikermi	Dytico	Italy		S.E.-Asia	S.W.-Asia	Africa
Occ.n.l.	150*	170*	170*	165 *	150*	116–146	126–162	120–176
mean						132	142	147
n	1	1	1	1	1	74	12 + 26**	36
Bar.l.	137	160	159	155	–	96–122	116–135	111–156
mean						111	125	133
n						70	8	30
Na.l./Bar.l.	66 %	–	–	57 %	–	47–74 %	49–59 %	58–77 %
mean						59 %	54 %	68 %
n						69	9	29
Na.l./Occ.n.l.	60 %	–	–	54 %	60 %	40–61 %	45–56 %	55–72 %
mean						50 %	50 %	62 %
n						73	40	31
Na.w./Zyg.w.	58 %	–	–	60 %*	64 %	37–62 %	47–55 %	62–82 %
mean						48 %	50 %	71 %
n						75	9	29
Ht./Occ.n.l.	37 %	35 %*	41 %	(39 %)	(55 %)	31–41 %	37–46 %	42–50 %
mean						36 %	40 %	46 %
n						74	8 + 26**	29
Ht./Bar.l.	41 %	37%*	44 %	(42 %)	(53 %)	38–49 %	39–46 %	44–55 %
mean						43 %	43 %	51 %
n	1					70	9	29

F, respectively) illustrate the increase of the occlusal width with progressive wear (see discussion). The enamel height of these teeth in situ could not be established with certainty. BONIS et al. (1988) assign Dytico-3 to MN 13, suggesting a considerable age difference to the Pikermi material. However, there is no reason to doubt the allocation to *H. primigenia*.

Bayirköy (Turkey): The mandible without number in the collection of the MTA from the Late Turolian was mentioned by ÜNAY & DE BRUIJN (1984) as *Hystrix* species. The incisor width (5.9 mm), the tooth row length, and the dimensions of the cheek teeth (Tab. 3) are within the range or smaller than the specimens from Pikermi. Their relative height is within the range of the Pikermi sample (Tab. 3). The wear class of the p4 agrees with the three folds found in class Q of the basic pattern but it has one island more, the m1 is in between S4 and T2, the m2 and m3 are class S4. This specimen cannot be distinguished from *H. primigenia*.

Gülpınar (Turkey): In the p4 of a mandible fragment (MTA, without catalogue no.) with p4–m2, the buccal fold and a lingual fold are present. This fits class R, but instead of three islands, five islands are developed. The m1 with 6 islands fits class S4. The m2, just like the p4, fits with its two folds class R, but has also five islands. The p4, 11.5 mm long, is slightly longer than the Pikermi series, and the m2 is slightly broader (Tab. 3). The relative height of the m1/2 is at 55 % and 59 %, respectively, not significantly different from the mean (54 %) of the Pikermi sample. We therefore assign this specimen to *H. primigenia*.

Kemiklitepe (Turkey): The finds from the Middle Turolian (MN 12) of Kemiklitepe (SEN 1994) are similar or slightly larger than the Pikermi specimens (Tab. 3). The relative height of the teeth of this material agrees with the Pikermi sample, confirming SEN's allocation of this material to *H. primigenia*. The influence of attrition in this sample is illustrated by the lowest tooth

(M2, relative height 42 %, wear class G8) opposed to the highest one (P4, 94 %, class D). The extreme width of one M3 (12.7 mm) is due to its stage of wear (see discussion).

Şerefköy, Muğla-Yatağan (Turkey): From this locality is a left mandible fragment (MTA, without catalogue no.) with p4–m3 in a very advanced stage of attrition with the wear classes T1, T3, T1 and T2. An upper incisor fragment from this locality has a width of 6.4 mm, which is within the range of the Pikermi specimens. The length of the tooth row and the length of the p4 and m1/2 (Tab. 3) do not differ from the Pikermi specimens, and only m3 is larger. The m1/2 and m3 are broader, which may be related to the very extensive wear. The relative height of all these teeth is clearly lower than in the Pikermi series. This is obviously also correlated with the advanced wear of these teeth. ATALAY (1980) mentioned a Turolian age for this specimen, which he allocated to *H. primigenia*, as is done here.

Taraklia (Moldavia): A skull fragment from Taraklia was described by RIABININ (1929) under the name *H. bessarabica*. About its age only RIABININ's communication "La faune est du type de celle de Pikermi" is known. The teeth of the right P4 – M3 series show the wear classes D/E, G1, F4 and D/E, respectively, the left M2 class E3 and the M3 class D/E. This specimen (Tab. 3) is slightly, but not significantly, smaller than those from Pikermi. From this specimen no enamel height measurements are available, but x-ray photographs show that the enamel crowns are not higher than the length of the cheek teeth. For the right M2 with wear class F4 the relative enamel height is estimated at 95%. That of the M1 is clearly lower, so the specimen is allocated to *H. primigenia*.

Siwaliks (India): LYDEKKER (1878) described a mandible fragment, GSIC D 96, from Hasnot, Siwaliks, India, under the name *H. sivalensis* (Figs. 4C1–C3). The dp4 and m3 are lacking, but the length of the tooth row (39.5 mm) could be measured at the alveoli. The length of this young specimen may be somewhat smaller than in full-grown specimens, but is not essentially different from *H. primigenia*. Neither the m1 length (9.6 mm) nor its absolute (7.4 mm) and relative (77 %) enamel height differs from this species. BARRY & FLYNN (1990) attributed an age of 7.0 Ma to this specimen which agrees with Late Turolian (MN 12). This specimen cannot be distinguished from *H. primigenia*.

Material allocated to *Hystrix depereti*

Perpignan (France): Occlusal patterns of the lower cheek teeth. – In the mandible fragment of *H. depereti*, MMPE PR 24 (Figs. 5A-B), the p4 shows two folds as in class R, but the presence of four islands instead of the
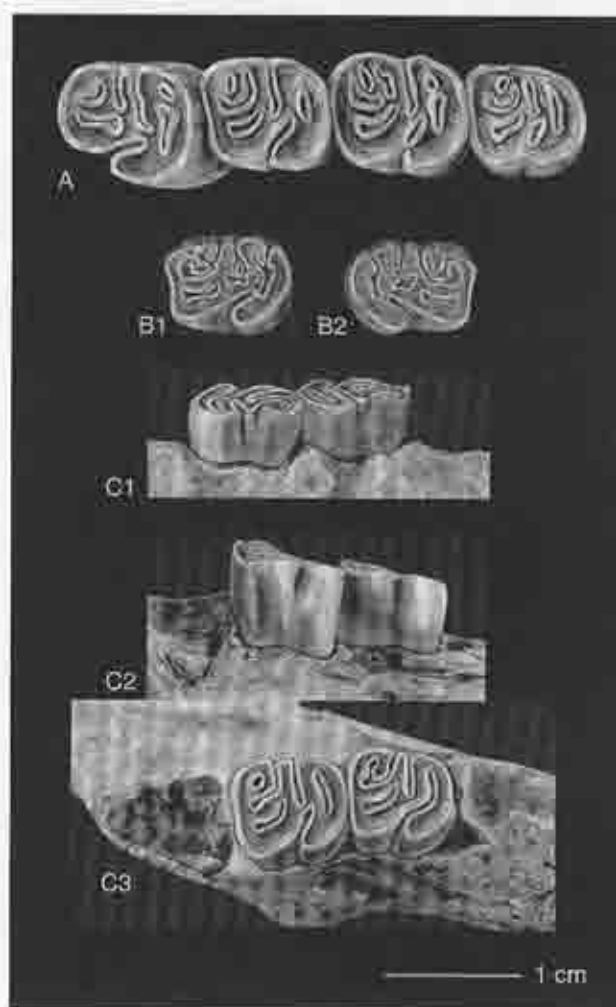

Fig. 4. – **A:** Occlusal view of the p4-m3 of the right mandible MNLP Pik.3089 (GAUDRY 1862: pl. 18 fig. 4) from Pikermi, figured as a left one. – **B1:** right, and **B2:** left m1 of DPUA Pik.G.44, Pikermi. – **C1:** lingual, **C2:** buccal and **C3:** occlusal view of the right mandible fragment GSIC D96, holotype of *Hystrix sivalensis* LYDEKKER, 1878, Siwaliks, India, figured as a left one.

maximum of three, corresponds to class S (Tab. 1). In the mandible fragment MMPE PR 25, the m2 has two folds, fitting in class R too, but its five islands instead of maximal three also suits class S1. This relatively large number of structural elements is also present in the specimens MMLY Pp55 and MMLY Pp58a. This feature cannot be established in less worn cheek teeth of class O, and it is no longer present in the more advanced stages of wear of class T. The conclusion is that these lower cheek teeth from Perpignan reflect the basic pattern of extant *Hystrix* species, but on average a larger number of structural elements occurs in most stages of wear. This feature can also be observed in the material from Pikermi.

The mandible fragment MNLP Pik.3089 (Fig. 4A) from the type locality Pikermi of *H. primigenia* has a p4 with three folds which agrees with wear class Q, but it has four enamel islands instead of one in that class. The m1 of that mandible agrees with class R in its single buc-
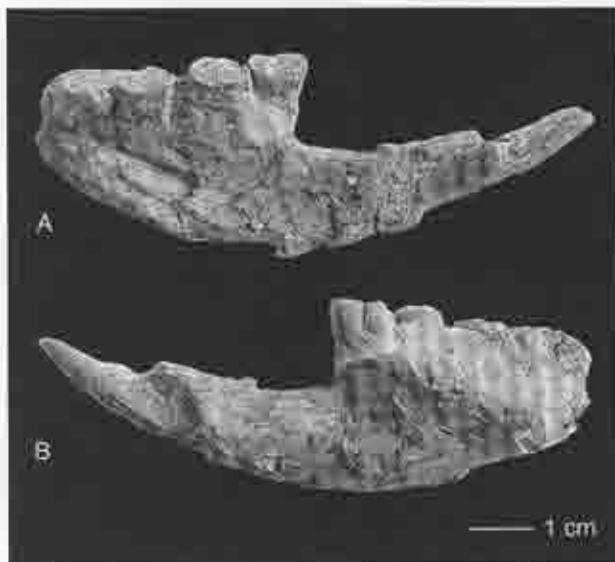
Fig. 5. – A: lingual, and B: buccal view of left mandible MMPE PR24 with p4-m3 (DEPÉRET 1890: pl. 4 fig. 12), of *Hystrix depereti* from Perpignan.

cal and lingual fold, but it has three anterior islands instead of two in that class. The m2 looks most like wear class S, but it has seven islands instead of six in that class. In the subadult mandible fragment PGUA-Pik.G44 from Pikermi, the left m1 (Fig. 4B-1) can be referred to class P. However, it differs in the presence of not only four lingual folds instead of two, but also in the presence of an extra island. The right m1 (Fig. 4B-2) of that mandible shows the same pattern. This relatively large number of occlusal elements occurs also in most of the teeth of the mandible fragments UPGM ASII145 and PGUA Pik.G43 from Pikermi. So no differences can be shown between the occlusal morphology of the lower cheek teeth of *H. depereti* and *H. primigenia*.

Occlusal patterns of the upper cheek teeth: – The patterns of the two P4 from Perpignan fit class D, three M1/2 in D, E and F, and two M1/2 in class G. So these five available upper teeth do not differ from the basic pattern in extant *Hystrix* species.

The upper tooth row of the skull (UPGM ASII144) from the type locality Pikermi (Fig. 6A) has a P4 with an occlusal pattern that only differs from class G4 by its open second buccal fold instead of a closed one (Tab. 1). The M1 shows class G4, the M2 differs from class G4 only in the third buccal fold being still just open instead of closed, and the M3 fits class D in its number of folds and islands. The maxillary fragment (MNLP Pik.3116) from Pikermi (GAUDRY 1862: pl. 18 fig. 3) has a P4 of class E, the M1 is class G4, the M2 and M3, respectively, are in F and E. So the upper cheek teeth from Perpignan as well as from Pikermi show the same basic pattern of the extant *H. brachyura*, or represent only minor variations. The overall conclusion is that no differences can be shown in the occlusal morphology between *H. depereti* and *H. primigenia*.

Fig. 6. – A: occlusal view of the P4-M3 of skull IPGM ASII144 from Pikermi, Greece. – B: occlusal view of four isolated upper molars without catalogue nos., coll. E. ÜNAY, Çoban Pınar, Turkey. – C1: Occlusal view of the left DP4-M3 of skull AMNH 20551, C2: lingual view of the M1, C3: lingual view of the M2 of that tooth series.

Remarks: – SEN (2001a) allocated two specimens from Perpignan (PR-153 and PR-156) to *Hystrix* cf. *primigenia* based on the basis of smaller size, lower height of crown, and some features of the occlusal surface. PR-156 was identified as an m1 or m2. This specimen has a length of 10.5 mm and enamel height of 10.6 mm. It is certainly a lower cheek tooth with a clear, wide and high, anterior contact facet. Posteriorly it has a rounded outline without a trace of a contact facet. Moreover, its relative enamel height (101 %) differs clearly from the m1/2 sample from Pikermi (39–72 %, n = 7). Therefore, this tooth is considered an m3, representing the upper end of the range (9.6–10.5 mm) in the Perpignan sample (mean 10.0 mm, n = 5). The occlusal pattern is quite common in *Hystrix* and fits wear class P1 as figured by VAN WEERS (1990: pl. 2 fig. 10), so this specimen can undoubtedly be allocated to *H. depereti*. Specimen PR-156 is an M1/2, the length of which (10.2 mm) just exceeds the Pikermi range (9.0–10.0 mm) and
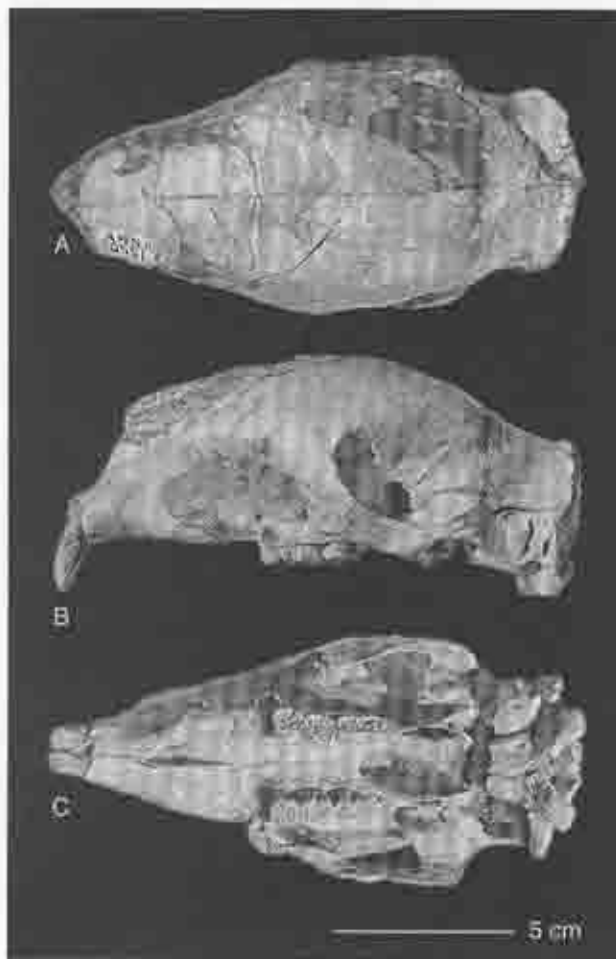
Fig. 7. – A: upper, B: left, and C: lower view of skull AMNH 20551 from Samos, Greece. – Photographs by W.A. DEN HARTOG, Utrecht.

Tab. 6. Measurements of the cheek teeth of the skull from Samos (AMNH 20551). – Abbreviations as in Tab. 2.

	W	L	EH	EH/L	CI
dP4	8.3	9.4	6.0	64 %	C/D
M1	8.9	9.9	11.6	117 %	C3
M2	9.2	10.0	13.3	133 %	B3/4
M3	–	–	–	–	in alv.

mandible fragment (AMNH 23030) with the incisor and a part of the m3 only. The Samos skull, a sub-adult specimen, has an estimated occipito-nasal length of 150 mm (Tab. 5). The adult size can be estimated by comparison with skulls of extant *H. cristata*. Measurements of 12 subadult and 36 adult skulls of *H. cristata* show that the adult size of the Samos skull may have been about 170 mm, the same as adult specimens from Pikermi and Dytico (Tab. 5).

Cheek tooth morphology: – The occlusal pattern of the tooth row of the skull AMNH 20551 from Samos is shown in Fig. 6C-1, lingual views of the M1 and M2 in Figs. 6C-2 and 6C-3, and dimensions of the cheek teeth are given in Tab. 6. On the length of the M1 and M2 alone it cannot be judged, if the skull from Samos agrees with either the specimens from Pikermi or Perpignan. The alveolar length of the tooth row (36 mm) with the decidious premolar and the scarcely erupted M3, is not indicative either. However, these teeth with relative enamel heights of 117 % and 133 % are clearly higher than the teeth from Pikermi (68–80 %, n = 4) and agree better with those from Perpignan (62–120 %, n = 5) and Węże (106 and 150 %, n = 2). On the basis of greater enamel height, the skull from Samos is allocated to *H. depereti*.

Skull height and nasal dimensions: – The Samos skull has about the same relative height as the *H. primigenia* skulls from Pikermi and Dytico. It agrees well with *H. brachyura* also, but is probably lower than *H. indica* (Tab. 5). A comparison of the nasal structure with that of *H. primigenia* cannot be made due to lack of nasal measurements of the skulls from Pikermi and Dytico. The nasal length of the Samos skull is 60 % of the occipito-nasal length (Tab. 5), so it is larger than the mean of *H. (Acanthion) brachyura* (50 %, n = 73), and is larger than the largest specimen of *H. (Hystrix) indica* (56 %), and reaches the lower part of the range of *H. cristata*. The same holds for the width of the nasals of the Samos skull, but these bones do not reach the extreme development of the nasal width of *H. cristata*. The Samos nasals may be larger or about the same as in *H. refossa*, but the height of the skull is probably less than that of *H. refossa*.

Çoban Pınar (Turkey): Occlusal patterns: – Eight isolated unnumbered upper cheek teeth (MTA) from Çoban Pınar in an early stage of wear are considered to come

falls within the Perpignan range (9.6–10.8 mm, n = 5). Its occlusal pattern is not common, the wear class is about between D and E, but this variation is often seen in *Hystrix*. Its relative enamel height (101 %) is within the range of the M1/2 of Perpignan (62–120 %, n = 5) and differs from that of Pikermi (70–80 %, n = 4), so there is no reason to doubt allocation to *H. depereti*.

Teruel (Spain): One M1/2 from Villastar, Teruel, Spain, DSTL coll. P. MEIN, has been dated to the middle part of the Late Turolian, MN 13 (MEIN et al. 1990). This tooth has a width of 10.4 mm, length 11.8 mm, enamel height 15.3 mm, and wear class C. The length and the enamel height of this tooth (129.7 % of the length) are clearly above the range of the Pikermi teeth. This specimen is allocated to *H. depereti*.

Samos (Greece): Skull size: – The skull AMNH 20551 from the island Samos (Figs. 7A-C), listed by SOLOUNIAS (1981) as *H. primigenia*, was figured in an unpublished report (BAKR 1959). Only the anterior part of the nasal bones of this nearly complete and little deformed skull is missing. Other material from Samos is the left

from the dentition of one specimen on similarities of most of the occlusal patterns. However, some differences between the left and the right teeth from the same position occur. The P4 of the left series (Fig. 6B) shows an uncommon occlusal pattern with the lingual fold already missing while the four buccal folds are still present, a wear stage comparable with class C. The M1 shows a pattern between C and D, the M2 has wear class D5, but the lingual fold is still connected with the second buccal fold. The M3 agrees with class C3, but also there the lingual and second buccal fold are connected. These patterns are not common but may be individual variations.

Tooth dimensions: – The length of 40.5 mm of the P4-M3 (Tab. 4) is an estimated value and not significantly different from the Pikermi specimens. The measurements of the P4 and M3 are given separately because of the differences between the left and the right ones in the same position. Most of the cheek teeth from Çoban Pınar (Tab. 4) are larger than those from Pikermi (Tab. 3) so they suggest a larger species than the Pikermi porcupine. The relatively narrow P4, M1, and M2 may be explained by their early stage of wear.

Enamel height: – Not all the cheek teeth from Çoban Pınar are higher than those from Pikermi when their early stage of wear is taken into account. Only one M1/2 (107 %) and two M3 (105 and 108 %) have relative enamel heights above 100 % (Tab. 4). However, none of the upper cheek teeth in any stage of wear in the assemblage from Pikermi exceeds a relative enamel height of 100 %. OZANSOY (1965) mentioned a Late Miocene age for the fauna from Çoban Pınar and compared it with that of Pikermi, but based on the relatively larger size and on greater average tooth height these specimens are allocated to *H. depereti*.

Węże (Poland): Size and tooth height: – The length of the upper and lower cheek teeth, and consequently the length of the tooth series (Tab. 4), is clearly greater than in the Pikermi sample (Tab. 3). The same holds for the relative enamel height of these teeth, so this material is allocated to *H. depereti*.

Occlusal patterns: – SEN (2001b) suggested already that the Węże specimens should not be included in *H. primigenia*, but probably represent a new species, in part based on the presence of five buccal folds and an antero-lingual fold in the P4 described by SULIMSKY (1960: fig. 1). This P4 is the only available one, and its occlusal morphology may reflect its early stage of wear (class B1). One of the four M1/2 studied has class A, one of them C, one D and one class F. So these upper teeth from Węże do not differ from the basic pattern of *Hystrix*. Hence the significance of a complicated structure of the P4 has to await the availability of more specimens. The one p4 available from Węże shows an extra island for class Q, a feature known to occur in the Pikermi as well as the Perpignan teeth. The five m1/2 are either too worn or not worn enough to confirm SULIMSKY's (1960) observation of a different dental morphology.

Brisighella (Italy): MASINI & ROOK (1993) described the *Hystrix* material from the rich faunal assemblage from latest Messinian (MN 13) fissure fillings at Brisighella, Italy. The relative enamel height (Tab. 4) of the upper cheek teeth (121–132 %) and the length of the lower tooth series (46.9 mm) clearly exceed *H. primigenia*. The p4 in that series is not high (76 %), but this agrees with its wear stage of class R/S, and the same holds for an m1/2 with 82 % in class T1 and an m3 with 67 % in class S4. This material is therefore allocated to *H. depereti*.

Kalimanci (Bulgaria): A relatively large collection of remains was described by SEN & KOVATCHEF (1987) from the latest Miocene of Kalimanci, Bulgaria, allocated to *H. primigenia* and kept in the private collection of the second author. Tab. 4 shows that most of the teeth are larger than those from Pikermi and within the range of the Perpignan material. Unfortunately, no height measurements are available, and enamel height measurements from casts (MNLP) are not reliable. On the data available, this material is assigned to *H. depereti*.

Menacer (Algeria): ARAMBOURG (1959) mentioned five isolated cheek teeth from Menacer, formerly Marceau, Algeria, and figured four of them. THOMAS & PETTER (1986) mentioned a Turolian age for these finds. The length of the P4 (Tab. 4) in this series exceeds the two from Pikermi. The mean of the two M1/2 (10.25 mm) exceeds the series from Pikermi (mean 9.6 mm, n = 4). The two m1/2 do not differ from the Pikermi sample (n = 9). These measurements suggest a slightly larger average size of the form from Menacer.

The P4 (Tab. 4) has a relative enamel height of 116 % compared to 91 and 93 % of the two from Pikermi (Tab. 3). The two M1/2 teeth from Menacer have relative heights of 100 % and 103 %, compared to those from Pikermi 70 % to 80 % (n = 4). The two m1/2 teeth from Menacer have heights of 87 % and 70 %, those from Pikermi 39 % to 72 % (n = 7). Although these figures are not fully comparable because of the differences in stages of wear, they show that the Menacer finds represent on average higher crowned animals allocated to *H. depereti*.

Las Casiones (Spain): Tooth dimensions: – ALCALÁ & MONTOYA (1998) described porcupine remains from the upper Turolian of Las Casiones, Teruel, Spain, dated to the middle part of MN 13. They provided figures and a table (1998: tab. 1) with, among others, occlusal length, enamel height, and wear classes of the cheek teeth. From these data the relative enamel height of the cheek teeth has been calculated as given below. The P4 in the tooth row (KS-7) has an occlusal length of 12.6 mm and a width of 13 mm (ALCALÁ & MONTOYA 1998: tab. 1), which exceeds the size of all other P4's discussed in this study. The length of the four M1/2 in their series range

from 10.2 to 11.6 mm (mean 11.0 mm), so these are clearly larger than the specimens from Pikermi (mean 9.6 mm, n = 4). The one p4 (KS-122) with a length 11.3 mm has the same size as the Pikermi sample. The length of the three m1/2 ranges from 10.5 to 11.7 mm (mean 11.2 mm), so they are on average larger than the Pikermi series (mean 10.3 mm, n = 9). The length of one M3 (KS-7) with 10.9 mm and one m3 (KS-122) with 10.8 mm is greater than the longest in the Pikermi series (9.0 and 9.8 mm, respectively). So the dimensions of the upper as well the lower teeth suggest that the porcupine from Las Casiones is larger than that from Pikermi and has to be allocated to *H. depereti*.

Relative height: – The relative enamel heights, calculated from ALCALÁ & MONTOYA's (1998) data of the P4–M3 series (KS-7), are 86.5 %, 57.3 %, 70.2 %, and 84.4 % respectively. For the P4, the authors gave the wear of class E-F, but the occlusal surface of that tooth (ALCALÁ & MONTOYA 1998: pl. 1 fig. 7) in which the lingual fold has disappeared, suits wear class G. In this figure, the four buccal enamel islands seem to have lost contact with the outer enamel layer, so on this feature too, a wear class of G4 seems to fit better. This also agrees better with the nearly totally worn down M1 (wear class H) and the advanced stage of wear (G4) of the M2 and M3 of this tooth series. So the height of these teeth is not so small in relation to an advanced stage of wear. Two isolated M1/2 (KS-1 and K93-1078) with wear class C show relative enamel heights of 116.4 % and 123.8 %, respectively. Two isolated upper teeth of wear class C? (KS-52) and wear class A-B (KS-54) have enamel heights of 123.8 % and 178.9 %, respectively. In all upper teeth from Las Casiones, the enamel height varies from about 57 % to about 179 % of the tooth length. Tab. 3 shows that in the upper teeth from Pikermi, Dytico, Çoban Pınar and Kemiklitepe together, the enamel height varies from 42 % to 99 %. So the upper teeth of Las Casiones are not only larger but on average also higher than the teeth from Pikermi and those from the other localities mentioned, indicating to allocation to *H. depereti*.

The height of the lower teeth, however, seems to provide a contrary indication. For the teeth of the p4–m3 tooth row (KS-122), the enamel heights of 71.7 %, 54.3 %, 55.6 %, and 56.5 % are calculated, and for the one isolated m1/2 (K93-1003) 65.8 %. All the lower cheek teeth from Pikermi (Tab. 3) range from 39 % to 97 %, so the teeth from Las Casiones fall within that range. This contradictory indication may be due to the fact that the four lower cheek teeth in the mandible KS-122 cannot be measured accurately, whereas the cheek teeth with the larger enamel height mentioned above are all isolated specimens. Moreover, for the fifth lower tooth mentioned, the isolated m1 (K93-1003), an enamel height of 65.8 % is calculated from ALCALÁ & MONTOYA's (1998) measurements, but their figures (pl. 1 figs. 5, 6) suggest a larger height. The larger size of all the cheek teeth from Las Casiones and the enamel height

Tab. 7. Measurements of *Hystrix aryanensis* SEN, 2000. – Abbreviations as in Tab. 2.

| | Mol. 51 | | Mol. 52 |
	Left	Right	Left
M1 L	8.7	8.8	9.0
W	7.9	8.0	9.6
EH	10.0	9.5	10.5
E/L	115	108	117
CI	D5	D5	C3
M2 L	8.5	8.5	9.0
W	8.1	8.1	9.5
EH	9.2	–	12.3
E/L	108	–	137
CI	B1	B1	C3

of the majority of them indicate assignment to *H. depereti*.

Material allocated to *Hystrix aryanensis* SEN, 2001

Tooth dimensions: SEN (2001b) described the new species *H. aryanensis* based on skull fragments of a young and a subadult specimen from the Late Miocene, Middle Turolian, of Molayan, Afghanistan. This species is clearly smaller (Tab. 7) than *H. primigenia*. Sen described the upper cheek teeth as "quite low crowned". However, the relative enamel height of the five M1/2 of the two specimens (range 108–137 %, mean 117 %) is higher than in the Pikermi sample (Tab. 2), on average higher than in *H. parvae* (mean 107 %, n = 8, VAN WEERS & MONTOYA 1996), and fall within the range of *H. depereti* (Tab. 8). However, SEN (2001a) mentioned "semi-hypsodont cheek teeth" in his diagnosis of the latter species, showing again the unsuitability of these subjective terms. *H. aryanensis* is the third species known from the Late Miocene, and it indicates that increase of tooth height occurred already in the Middle Turolian.

Occlusal pattern: SEN (2001b) described the unusual presence of a strong connection between the syncline II and the sinus, or between the second buccal and the lingual fold in our terminology. This connection is also defined in wear class D1 (VAN WEERS 1990), but in the M1 of the holotype specimen MOL-51 the stage of attrition is further advanced with two islands developed instead of one in class D1, which makes the presence of this connection more striking. The presence of this connection in the M2 of this tooth row is not uncommon in its early stage of wear (B1), but in the M1 of MOL-52 the connection is still clearly present, although this dentition is farther developed with the dP4 already shed. Remarkable enough, in the M2 of that tooth row, although in a less advanced stage of attrition than the M1, the connection between the lingual fold and the second buccal fold is lacking. More specimens are needed to show, if this is
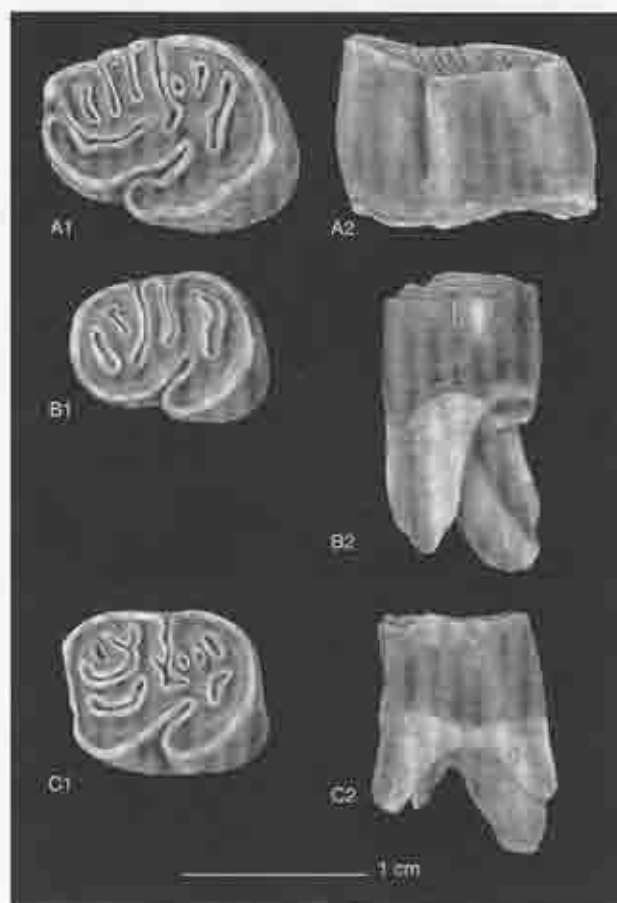
Tab. 8. Ranges and means of measurements of specimens allocated to *Hystrix primigenia* and *Hystrix depereti*. – Abbreviations as in Tab. 2.

	H. primigenia mean (n) range	*H. depereti* mean (n) range
P4–M3	39.2 (5) 38.2–41.0	43.2 (3) 40.5–45.0
P4 L	10.9 (5) 10.1–11.5	11.7 (6) 11.0–12.5
EH	9.8 (5) 8.5–10.5	12.3 (3) 10.9–14.5
E/L	89 (5) 74–94	110 (3) 97–132
M1/2 L	9.4 (12) 8.7–10.0	10.2 (19) 9.2–11.2
EH	6.3 (8) 3.8–8.0	10.4 (11) 6.2–14.7
E/L	67 (8) 42–80	105 (11) 62–150
M3 L	8.6 (7) 8.0–9.3	9.3 (6) 8.7–10.0
EH	6.9 (5) 4.8–7.9	(1) 10.5
E/L	80 (5) 52–99	(1) 121
p4–m3	40.0 (5) 38.2–43.4	46.4 (4) 44.0–47.5
p4 L	11.3 (8) 10.7–12.2	12.4 (8) 10.7–13.2
EH	7.6 (8) 3.9–10.6	11.0 (7) 9.3–15.3
E/L	68 (8) 35–95	87 (7) 72–116
m1/2 L	10.2 (15) 8.8–11.6	11.3 (22) 10.2–13.1
EH	5.1 (13) 2.5–8.4	8.7 (17) 2.4–14.8
E/L	51 (13) 23–72	77 (17) 22–144
m3 L	9.8 (5) 9.4–10.4	10.2 (8) 9.6–10.8
EH	5.5 (5) 3.0–9.5	8.1 (6) 4.7–11.8
E/L	56 (5) 29–97	78 (6) 46–109

Fig. 8. Cheek teeth HGIB ob-4619A–C from Polgárdi, Hungary. – **A1:** occlusal and **A2:** buccal view of the left p4 4619-A. – **B1:** occlusal and **B2:** lingual view of the right p4 4619-B, figured as a left one. – **C1:** occlusal and **C2:** lingual view of the right m1/2 4619-C, figured as a left one. – Photographs by L.A. V.D. LAAN, Amsterdam.

a stable diagnostic character for this species or if it represents an example of the notorious intraspecific variation in this genus.

Material from Polgárdi allocated to *Hystrix* sp. indet.

Occlusal patterns of the cheek teeth: A collection of 7 molars from the Late Miocene, Turolian (MN13) of Polgárdi, Hungary (HGIB-ob–4619, A-G), were allocated to *Hystrix* cf. *primigenia* by KORMOS (1911), but not described. Specimen 4619-A (Figs. 8A-1 and 8A-2) is a left p4 with one relatively deep anterior enamel fold, three lingual folds, one buccal fold, one anterior, and three posterior islands. This complex pattern is significantly different from all other *Hystrix* teeth studied, and the basic plan cannot unambiguously be recognized in it. Specimen 4619-B (Figs. 8B-1 and 8B-2) is a right p4 that, with its occlusal pattern of three folds, can be seen as class Q, but differs from it by the presence of three islands instead of one. Specimen 4619-C (Figs. 8C-1 and 8C-2) is an m1 with a lingual and a buccal fold and 7 islands. The antero-lingual island seems to be homologous with the anterior fold of specimen 4619-A, and in the large number of structural elements it looks like that tooth as well. Specimen 4619-D is an M3 that fully complies with the basic pattern of class G5, and the same holds for 4619-E, an M1/2 of class G1. An unworn spec-

imen (4619-F) may be an m1/2, and a seventh specimen (4619-G) is poorly preserved and is probably not *Hystrix*. The complicated occlusal morphology of teeth 4619-A and C recalls the beaver *Anchitheriomys* ROGER, 1898. However, the seven incisors, also belonging to the collection from Polgárdi, are quite different from that of *Anchitheriomys* and have the morphology and enamel microstructure of *Hystrix* teeth (W. VON KOENIGSWALD, in letter 28-2-1994). It could be supposed that the teeth B, D and E belong to the same species as A and C and that the less complicated occlusal pattern of the former has to be explained by their more advanced stage of attrition. However, this morphology is significantly different from all other material. Moreover, there is a considerable difference in size.

Dimensions of the cheek teeth: The dimensions and wear class of five cheek teeth from Polgárdi are given in Tab. 9. The p4 (4619-A) in the Polgárdi series exceeds with a length of 13.5 mm the maximum in *H. primigenia* (11.3 mm) and the largest one of Perpignan (13.2 mm). The M1/2 4619-E, on the contrary, is with 8.4 mm tooth

Tab. 9. Measurements of five of the seven cheek teeth of collection HGIB Ob.4619 from Polgardi, Hungary. – Abbreviations as in Tab. 2.

4619	W	L	EH	E/L	CI
A (p4)	10.6	13.5	9.5	70 %	indet.
B (p4)	8.8	11.5	8.1	70 %	Q+
C (m1)	9.1	10.1	7.6	75 %	indet
D (M3)	8.8	8.5	6.0	71 %	G5
E (M1/2)	9.4	8.4	7.7	92 %	G1

length smaller than the Pikermi series. The serial position of the unworn tooth 4519-F (L 9.5 mm, W 9.1 mm) cannot be established, and tooth 4619-G (L 8.4 mm, W 7.3 mm) cannot be recognized as a porcupine. The width of the largest upper incisor out of the seven specimens in the Polgárdi collection (6.2 mm) falls within the range of the Pikermi series.

Taxonomic status: This collection of six cheek teeth is considered to represent a mixture of two species. The specimens 4619-A and 4619-C seem to be conspecific and could represent an undescribed *Hystrix* species. The length of the M1/2 no. 4619-E is too large to be allocated to *H. parvae* and below the range of *H. primigenia*. Based on its size and the relatively large enamel height of 92% in relation to the advanced wear (G1), this specimen and the slightly more worn M3 no. 4619-D could be allocated to *H. aryanensis* SEN, 2001. With the small number of specimens available and the poor knowledge of the ranges of variation of the species recognized thus far, it is not possible to allocate all these teeth.

Discussion

Taxonomic status of *Hystrix refossa* GERVAIS, 1852

Hystrix refossa GERVAIS, 1852 is based on a mandibular fragment with p4 from the Late Pliocene of Les Etouaires near Perrier, France. Besides the holotype, two M1/2 (coll. BRAVARD, BMNH 34958 and 34959) are available from the type locality. These specimens show that *H. refossa* is a large species, not much smaller than *H. primigenia* and *H. depereti*, but with a much higher enamel crown, up to nearly 200 % of the tooth length. Finds from seven other Plio-Pleistocene localities in Europe and from the Geula Cave in Israel cannot be distinguished from the Perrier material on dental characters and are allocated to *H. refossa* (VAN WEERS 1994). SEN (1999, 2001a) erroneously maintained the junior synonym *H. etrusca* BOSCO, 1898 for the large skulls with high-crowned teeth from Valdarno without any relevant argument. SEN (1999) applied the name *H. angressi* FRENKEL, 1970 to the extensive material from the Geula Cave because it is larger than the living species, but this equally holds for *H. refossa*. The cranial characters

mentioned by him are irrelevant for species distinction, so the name *H. refossa* is retained here in the concept of VAN WEERS (1994).

Increase of tooth height

SEN (1999) observed "the clear break in hypsodonty between the older species (*H. parvae* and *H. primigenia*) and the younger ones (*H. refossa, H. cristata* and *H. brachyura*)", concluding that "the hypsodonty rapidly increased sometime during the Pliocene". The difference in tooth height between *H. primigenia* and *H. depereti* shows that some increase in the Hystricidae occurred already much earlier. DE BRUIJN et al. (1990) place the Pikermi fauna in MN 12 and the material from Quarry 5 of Samos in MN 13. STEININGER et al. (1996) gave an inferred age of 8.3 to 8.2 Ma (MN 11/12) for the Pikermi fauna, and 7.3 to 7.1 Ma (late MN 12) for that of Q5 of Samos. So the increase in tooth height may have taken place in the Middle Turolian. This early tooth height development is not unique for *H. depereti*, as is apparent in the occurrence of *H. aryanensis* SEN, 2001 discussed above. In extant porcupines, the increase in tooth height and size is correlated with adaptations to dryer habitats and larger ecological and geographical ranges, such as the occurrence of species of the subgenus *Hystrix* s. str. in desert conditions. The larger geographical range of *H. depereti* than that of *H. primigenia* may be explained in this context.

Increase of the nasal region

The increase of the nasal size and skull height in Hystricidae results in a larger nasal cavity and obviously in an increase of the olfactory potential. This may be correlated with the well-known ability of *Hystrix* species to find underground food such as tubers and roots, apparently an adaptation to dryer habitats. The skull of *H. depereti* from Samos has about the same height as *H. (Acanthion) brachyura*, but it has nasals that are larger than the mean of this species (Tab. 5) and even larger than those of *H. (Hystrix) indica*. Judging by the morphology of the skull from Samos, *H. depereti* may have been adapted to a wider ecological range than *H. brachyura*.

Cheek tooth width

KOLIADIMOU & KOUFOS (1991) introduced the term "robusticity index" for the ratio between the occlusal width of the cheek teeth and the occlusal length. They noticed that this index is higher in *H. primigenia* than in *H. refossa*. DE BONIS et al. (1992) also used this ratio as a diagnostic character and listed a relative width of the M1 of the skull from Dytico of 137.4 %. VAN WEERS (1990, 1994) showed that such high ratios are due to a decrease of the length and increase of the width of the tooth in the course of attrition. This effect is caused by the tapering shape of the upper cheek tooth and the

changing angle of the occlusal surface as a result of pro-
gressing wear and axial curvature. The buccal side of the
occlusal surface consists in some cases of no more than
a very thin rim of enamel, causing a disproportionate
width of the tooth. The left and right M1 in the skull
from Dytico, both with wear class G7 and a relative
width of about 138 %, illustrate this feature. This index
may have diagnostic value for the comparison of larger
samples of specimens at the same stage of wear only.

Conclusions

*   The relatively low-crowned species *Hystrix primi-
    genia* occurred in SE Europe and Asia from the Early
    or Middle to the Late Turolian (MN 11/12 to MN 13).
*   *Hystrix depereti*, occurring from Spain to Turkey in
    the Middle Turolian (MN 12) to the Late Ruscinian
    (MN 15), differs from *H. primigenia* in its higher and
    on an average larger cheek teeth.
*   The occlusal patterns of the cheek teeth of *H. primi-
    genia* and *H. depereti* are the same. The lower cheek
    teeth of both species often show a slightly more com-
    plex pattern than the extant species.
*   *H. depereti* has a much larger area of distribution in
    Europe than *H. primigenia*.
*   The Late Miocene skulls from Pikermi and Dytico
    (*H. primigenia*) and from Samos (*H. depereti*) have
    about the same height as the extant species *H. (Acan-
    thion) brachyura*. The height of the skull of the Plio-
    Pleistocene *H. refossa* is greater, approaching *H.
    cristata*.
*   The nasals of the skull from Samos are larger than in
    H. brachyura and *H. indica*, but do not reach the level
    of development of *H. cristata*. The nasals of *H. refos-
    sa* are wider than those of the skull from Samos.
*   The difference between *H. primigenia* and *H. de-
    pereti* and the relative tooth height of *H. aryanensis*
    show that the increase in tooth height occurred al-
    ready as early as the Middle Turolian (MN 12).
*   The major increase of tooth height in *Hystrix* took
    place sometime during the Pliocene.
*   *Hystrix zhengi* differs from *H. primigenia* and *H. de-
    pereti* in its larger crown height of the p4. It differs
    from *H. depereti* in the smaller size of its p4.
*   The seven specimens from the Late Miocene (MN
    13) of Polgárdi, Hungary, represent more than one
    species.

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