The porcupine *Hystrix refossa* Gervais, 1852 from the Plio-Pleistocene of Europe, with notes on other fossil and extant species of the genus *Hystrix*

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Fossil *Hystrix* material from a large number of localities is biometrically analysed and compared with the extant species. *H. major, H. etrusca, H. makapensis,* and *H. angressi* are shown to be junior synonyms of *H. refossa. H. bessarabica* and *H. trofimovi* are shown to be junior synonyms of *H. primigenia,* and *H. schaubi* and *H. cristata minor* of *H. vinogradovi.* The dental characteristics of *H. refossa, H. primigenia* and *H. vinogradovi* are discussed.

Contents

Introduction

Most fossil species of *Hystrix* are based on small collections of teeth. Studies on the dentitions of extant species have shown that there is considerable intraspecific variation in the pattern of the occlusal surface and that this pattern changes as a result of attrition. Moreover the size of the occlusal surface is a function of the stage of wear. These circumstances in combination with the well-known conservatism of the hystricid dental pattern and the lack of knowledge of its ancestors have led to considerable confusion in the taxonomy of fossil Hystricidae. This study aims at sorting out the Plio-Pleistocene record of the genus *Hystrix* in Europe.

Hystrix refossa Gervais, 1852 is based on a fragment of a mandible with the P_4 and the alveoles of the M_1 from 'les alluvions anciennes et volcaniques des environs d'Issoire' (Tome I: 28-29, Tome II: 6-7, Tome III: pl. 48, fig. 11 and 11a, in Gervais, 1848-1852). Gervais (1859a) mentioned as the type locality 'les alluvions sous-volcaniques de la montagne de Perrier' and compared *H. refossa* with the extant species ('Taille du Porc-épic ordinaire'). The holotype is preserved in the Muséum d'Histoire Naturelle in Paris, and its label mentions 'les Etouaires (Perrier)'. The species name *H. refossa* has scarcely been used later.

Gervais (1859b) described some molars, incisor fragments and postcranial elements from the 'brèche de l'île de Ratoneau, près Marseille' as *H. major* and communicated that this species might be larger than the largest extant porcupine species of Africa and India. Gervais (1867-1869) gave measurements of incisor fragments and a metacarpal of this species and figured a molar, probably a lower one, but unfortunately without measurements. The age of the Ratoneau material is not known. Comparison of the holotype P_4 of *H. refossa* with the type material of *H. major* is unfortunately impossible because the latter could not be traced. Dr L. Ginsburg of the Laboratoire de Paléontologie in Paris kindly informed me (in litt., 13-III-1985 and 2-XII-1992) that he could not find the type of *H. major*. Professor Lavocat wrote to me (d.d. 15-IV-1985) that he also had not been able to locate the Ratoneau material in the fifties despite a thorough search, and that they were not mentioned in the 1955 catalogue of the museum of Paris. Inquiries made in relevant institutions in Montpellier, Lyon and Marseille all had a negative result. Therefore I consider the type material of *H. major* as lost.

Schlosser (1884) was the first to consider *H. major* a junior synonym of *H. refossa*, an opinion that was shared by Lydekker (1885), Harlé (1910) and Landry (1957). In spite of the doubtful status of *H. major*, this name has been applied to the *Hystrix* material from Osztramos-8 (Jánossy, 1972), Le Vallonet and Perrières (Chaline, 1972), Venta Micena (Agustí et al., 1987), and from Gerakou-1 (Koliadimou & Koufos, 1991). Recently, Masini & Rook (1993) characterised the status of *H. major* as: 'unsatisfactorily described ... never been accurately revised', and of *H. refossa* as: 'incompletely defined ... poorly known'.

Other sources of confusion are, that the differences between *H. refossa* and *H. primigenia* (Wagner, 1848), and between *H. refossa* and *H. vinogradovi* Argyropulo, 1941 have never been clearly established.

Two molars of *H. refossa* from the type locality Perrier in the collections of the British Museum add considerably to our information. The species *refossa* will be redefined and compared with relatively large samples of extant species as well as with the European Plio/Pleistocene material available.

Material and methods

Sources — Specimens from the following institutions have been studied:

BMNH	British Museum (Natural History), London;
DEUF	Dipartamento di Scienze della Terra, University of Firenze;
DSTL	Département des Sciences de la Terre, Lyon;
EIUR	Earth Science Institute, University of Roma;
HNHM	Hungarian Natural History Museum, Budapest;
HGIB	Hungarian Geological Institute, Budapest;
IPSB	Institute of Paleontology, Sabadell, Barcelona;
ISNB	Institut Royal des Sciences Naturelles, Bruxelles;
MACT	Musée Royal de l'Afrique Central, Tervuren;
MAKB	Museum Alexander König, Bonn;

MHNB	Muséum National d'Histoire Naturelle, Bâle;
MML	Muséum Municipal de Lyon;
MMP	Muséum Municipal de Perpignan;
MNLP	Muséum National, Laboratoire de Paléontologie, Paris;
MPVM	Museo di Paleontologia, Academy Valdarnese, Montevarchi;
MCM	Museo Civico di Storia Naturale di Milano;
MCV	Museo Civico di Storia Naturale, Verona;
NHMW	Naturhistorisches Museum, Wien;
NMP	National Museum, Praha;
RGM	Geological collections of Nationaal Natuurhistorisch Museum, Leiden (NNM);
SMF	Senckenberg Museum, Frankfurt am Main;
SMNS	Staatliches Museum für Naturkunde, Stuttgart;
UPGM	Universitäts-Institut für Paleontologie, München;
ZSM	Zoologische Staatssammlung, München;
ZMA	Zoological Museum, Amsterdam;
ZMB	Zoologisches Museum, Berlin;
ZMUF	Zoological Museum of the University of Firenze.

The extant species studied include 64 specimens of *H. cristata* Linnaeus, 1758, 19 of *H. africaeaustralis* Peters, 1852 and 17 of *H. indica* Kerr, 1792.

Measurements and terminology — The occlusal length (Fig. 1) and width of the cheek teeth have been measured with Vernier callipers. In the case of isolated teeth the height of a tooth with the root or roots was taken too, as defined by van Weers (1990; 1993, fig. 1).

By 'crown height' is generally understood the height of the enamel of a tooth. However, the enamel-dentine border is not always clear, especially in fossil specimens. It is sometimes covered with cement and this measurement requires an optical device. I therefore prefer to measure the distance between the occlusal surface and the point where the dentine splits up into two or more roots, with Vernier callipers (van Weers, 1993, fig. 1). This measurement of multi-rooted teeth differs somewhat from the enamel height, but it allows to quantify crown height. When the term 'crown' is used in this sense, it will be written in quotation marks.

Many cheek teeth of extant *Hystrix* species have a more or less cylindrical shape without branching of the dentine part. The large 'root', sometimes with two small vestigial rootlets, is in fact the continuation of the dentine body of the tooth. The degree of hypsodonty is expressed as the ratio of the total height and the occlusal length (Fig. 2) in those cases in which no 'crown' and root part can be distinguished. For multi-rooted teeth this ratio is used too. In some cases the ratio of the 'crown'-height/occlusal length as well as height/occlusal length is given. The occipito-nasal length of the skull as defined in van Weers (1976) and the alveolar and occlusal length of the upper and lower toothrows of adult specimens of the extant species of the subgenus *Hystrix* are presented in Table 1 for comparison.

If not otherwise indicated, all measurements given have been taken by the author.

Since the degree of attrition influences the dental pattern, the stage of wear of the

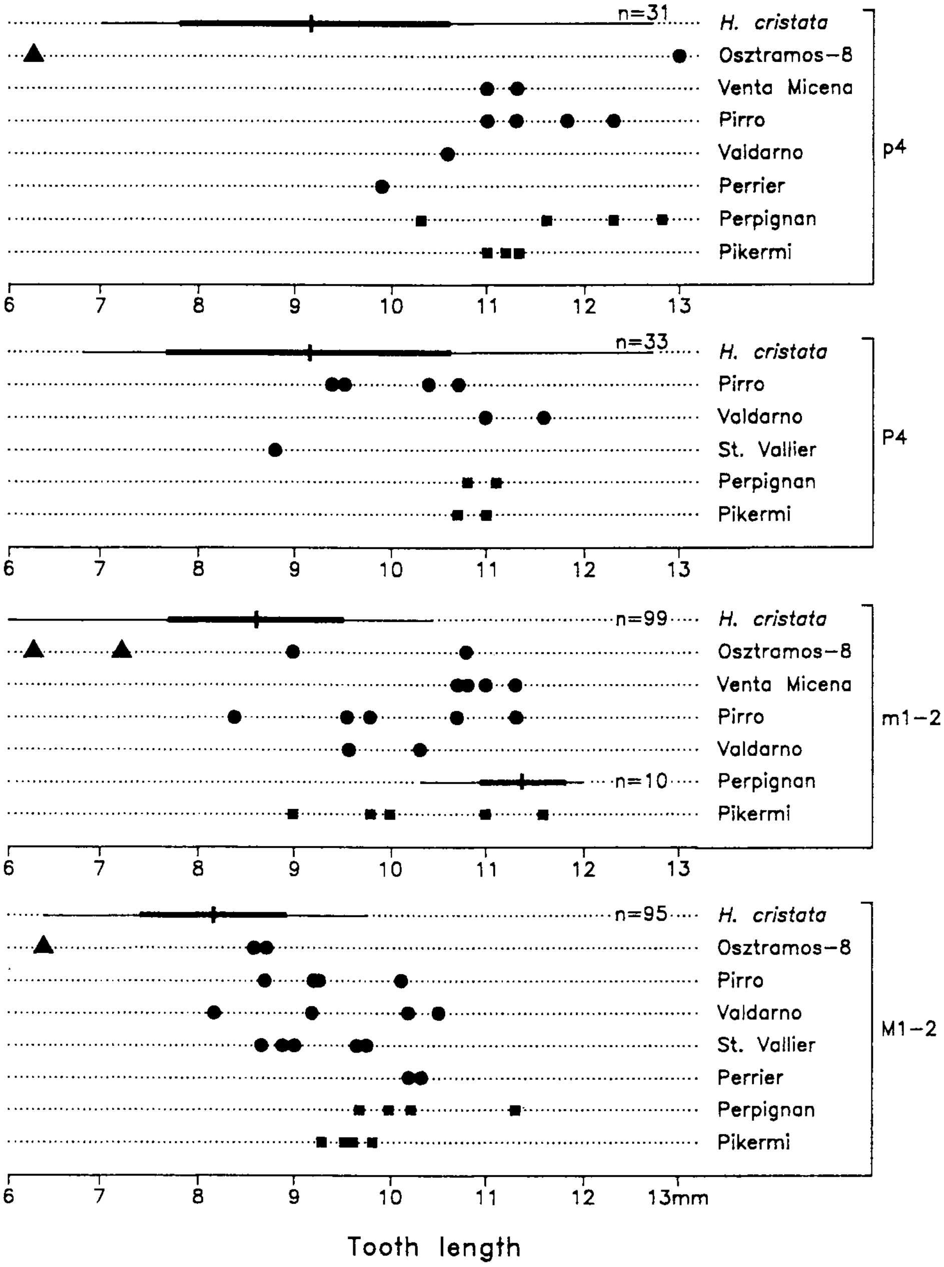

Fig. 1. Length in mm of M^{1-2}, M_{1-2}, P^4 and P_4 of fossil *Hystrix* and extant *H. cristata* specimens studied. Squares = *H. primigenia*, solid circles = *H. refossa*, triangles = *H. vinogradovi*, open circles = *H. cristata*. Samples of 10 and more specimens are represented with range, mean, 2 X the standard deviation, and sample size (n).

teeth is considered. To ensure comparison of teeth with approximately the same degree of attrition, the wear classes A to H for the upper, and O to T for the lower teeth were used as in van Weers (1990).

Taxonomy

Order RODENTIA Bowdich, 1821
Family Hystricidae Burnett, 1830
Genus *Hystrix* Linnaeus, 1758
Subgenus *Hystrix* Linnaeus, 1758

Hystrix (*Hystrix*) *refossa* Gervais, 1852

Synonyms — *H. major* Gervais, 1859; *H. etrusca* Bosco, 1898; *H. angressi* Frenkel, 1970; *H. makapensis* Greenwood, 1958.

Holotype — Fragment of a right mandible with P_4 and four alveoles of the M_1 roots, kept in MNLP, Pl. 1, figs. 1a-b, occlusal length of P_4 9.8 mm, greatest length = 9.9 mm, occlusal width 8.3 mm, greatest width 8.5 mm, height of visible crown enamel buccally 9.2 mm, lingually 7.8 mm, estimated total height with roots 14.5 to 15.6 mm. The tooth is in an advanced state of wear, class 'T', with 7 enamel islands in the occlusal surface.
Type locality — Les Etouaires, Perrier, Puy-de-Dôme, France.
Topotype material — Two M^{1-2}, BMNH 34958 and 34959, Bravard collection, purchased in 1854, Pl. 1, figs. 2-3, occlusal width 8.6 and 7.8 mm respectively, greatest width 9.0 and 9.5 mm, length 10.3 and 10.2 mm, height 20.3 and 19.8 mm, wear classes 'D5' and 'C3'.

Emended diagnosis — Very large-sized *Hystrix* with strongly hypsodont teeth.

Differential diagnosis — About the same size as *H. primigenia* but more hypsodont, index of height/occlusal length of all cheek teeth nearly always above 1.5 with maxima of up to 2.6, against rarely above 1.5 and maximum about 1.6 in *H. primigenia*. *H. refossa* is a clearly larger species than *H. indica* and on the average larger than *H. cristata* and *H. africaeaustralis*.

Age of the type locality — Late Pliocene, Villanyian, MN zone 16.

Stratigraphic range — Early Villanyian to Late Pleistocene.

Geographic range — See Fig. 3 for localities in Europe.

Discussion — In Fig. 1, the length of the holotype P_4 from Perrier is presented. This length of 9.9 mm differs less than one standard deviation from the mean of the *H. cristata* sample (n = 31). However, from this single observation it may not be concluded that the P_4 from Perrier belongs to a species of the size of *H. cristata*, as suggested by Gervais (1859a).

The exact height of the holotype P_4 cannot be established, but taking into account the advanced state of wear, it is clearly high-crowned. The M_1 of the holotype mandible must have had at least small roots, judging by the four alveoles in the mandible fragment. However, this also occurs in the extant *Hystrix* species with hypsodont teeth.

The length of 10.2 and 10.3 mm of the two upper molars from the type locality Perrier, mentioned by Lydekker (1885), is well above the maximum of 9.8 mm of the range of the sample of 95 *H. cristata* specimens (Fig. 1). From the four diagrams in

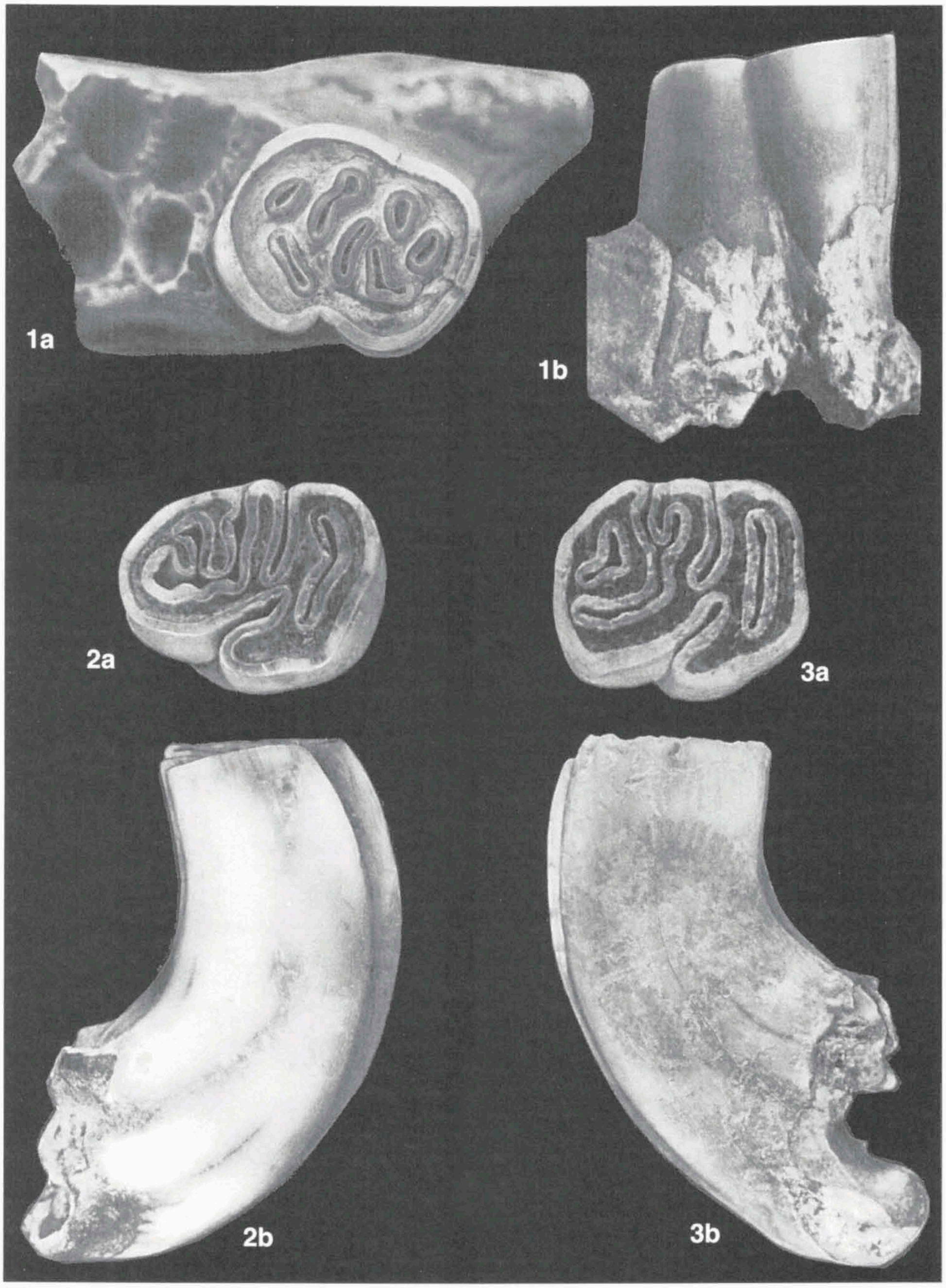

Plate 1. Dental elements.

Fig. 1. Mandible fragment with P_4 of *H. refossa*, holotype; a: occlusal view; b: buccal view. Fig. 2. Right M^{1-2} (BMNH 34959), topotype; a: occlusal view; b: posterior view. Fig. 3. Left M^{1-2} (BMNH 34958), figured as a right one, topotype; a: occlusal view; b: posterior view (3b). All figures approx. × 3.

Fig. 1, it appears that the samples from Perrier, St.Vallier, Valdarno, Pirro, Venta Micena, and Osztramos-8 represent a *Hystrix* with a larger mean size than *H. cristata*. The relatively small P^4 from St Vallier in Fig. 1 is an unworn and not yet erupted specimen.

The four diagrams of Fig. 2 show that the height of the cheek teeth of the assemblages from the localities mentioned are about equal, not different from *H. cristata*, and differing only from the teeth from Perpignan.

Comparison of toothrow lengths of specimens from Valdarno and Pirro in Table 2 with those of the extant species in Table 1 suggests that they represent a species that is on the average larger than *H. cristata*. Since the specimens from all the localities mentioned, except those from Perpignan, also have very similar dental patterns, they are considered to belong to one species, *H. refossa* Gervais, 1852, which has a larger mean size than the extant species and a similar hypsodonty.

The status of *H. major* Gervais, 1859 — The type material of this species is consi-

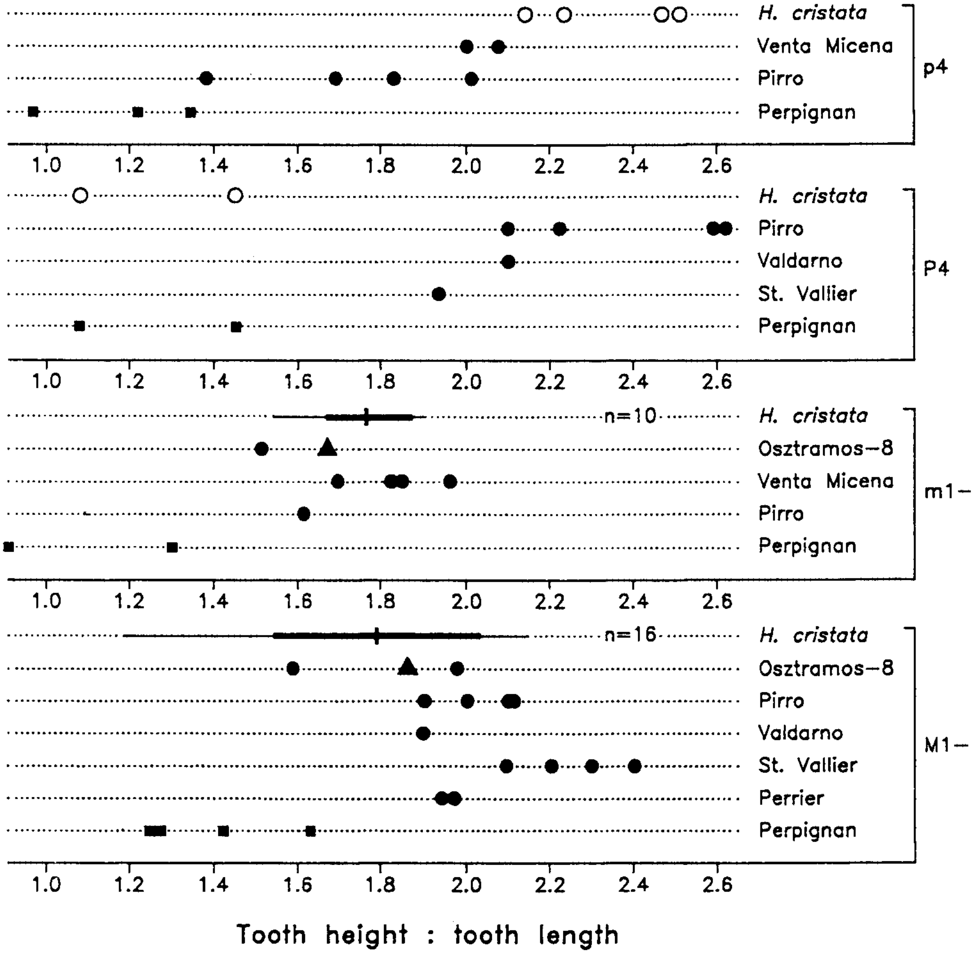

Fig. 2. Ratio 'tooth height/tooth length', of M^{1-2}, M_{1-2}, P^4 and P_4 of fossil *Hystrix* and of extant *H. cristata* specimens studied. Symbols as in Fig. 1.

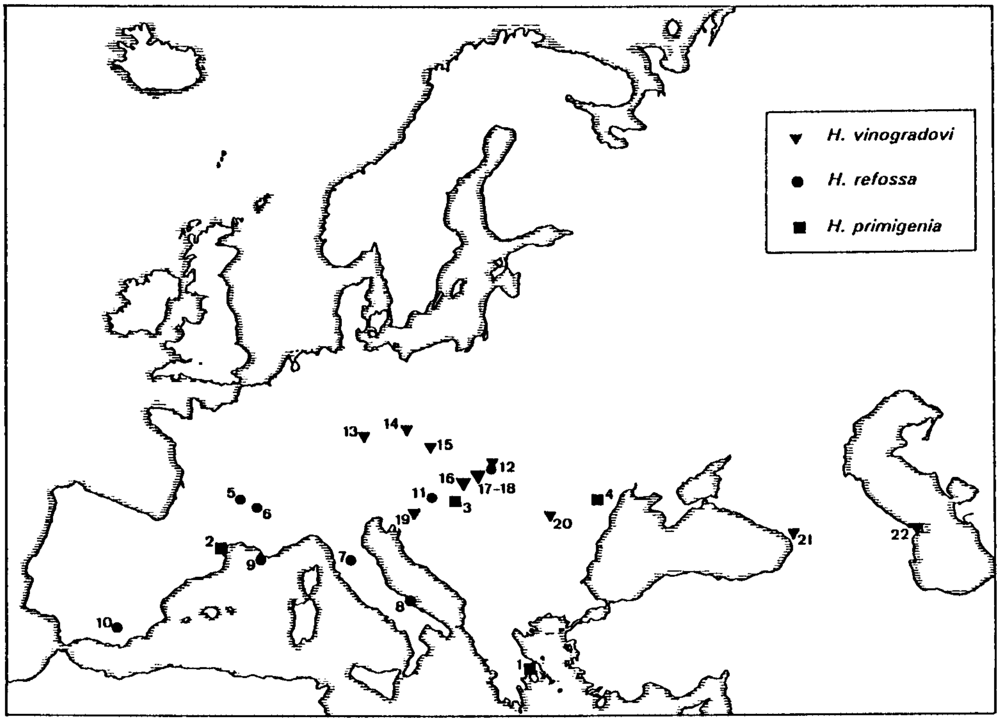

Fig. 3. Map showing the provenance of the fossil *Hystrix* specimens studied.
1 = Pikermi; 2 = Perpignan; 3 = Polgärdi; 4 = Tarakliya; 5 = Perrier; 6 = St. Vallier; 7 = Valdarno; 8 = Pirro Nord Quarry, Gargano; 9 = Ratonneau; 10 = Venta Micena; 11 = Gombaszög; 12 = Osztramos; 13 = Fuchsloch Cave, Siegmannsbrunn; 14 = Kotlarce; 15 = Ostrov; 16 = Csobánka near Budapest; 17 = Kiskohat; 18 = Lambrecht Cave, Varbó; 19 = Veternica Cave, Medvednica; 20 = Brassó; 21 = Kudaro; 22 = Binagady.

dered lost. The only information in the original description that is relevant for comparison is the size of an upper incisor. The width of 7 mm is well above the mean of *H. cristata* (6.1 mm) but does not exceed its range (5.3-7.3 mm, n = 15) in my files. The only other dimension of *H. major* given by Gervais (1867-1869) is the length of a rather large metacarpus (38 mm), but this does not provide an argument that it would be a larger species than *H. refossa* because specimens for comparison are not available. Depéret (1890), who apparently studied the type material of *H. major*, mentioned that it is 'presque aussi gros que l'*H. primigenia*', but this also applies to *H. refossa*. Since there is no indication that *H. major* differs from *H. refossa*, *H. major* is considered a junior synonyn of *H. refossa*.

The status of *H. etrusca* Bosco, 1898 — This species was described on the basis of two skulls (MPVM A and B) from the Early Pleistocene of Upper Valdarno. Skull A is dorso-ventrally compressed with an incomplete nasal region, and skull B is laterally compressed, and misses the occipital region. The stage of wear of the dentitions of both Valdarno skulls is the same and the palatal lengths of the skulls, 100 and 102 mm respectively, differ very little. It is therefore supposed that the other dimensions of these skulls differ very little too. Their measurements are presented (Table 3) as if

Table 1. Occipito-nasal length, alveolar and occlusal length of upper and lower toothrow in mm of adult specimens of the subgenus *Hystrix*: *H. cristata*, *H. africaeaustralis* and *H. indica*, with range, mean, number of specimens (n) and standard deviation (s.d.).

	H. cristata	*H. africae-australis*	*H. indica*
ccipito-nasal	120.0-175.6	141.4-163.0	126.0-158.0
length	146.7	150.0	138.7
n	37	12	13
s.d.	15.6	7.0	9.3
Alveolar length	27.7-42.5	32.1-38.8	29.6-34.8
of P^4-M^3	33.8	35.5	32.4
n	35	14	11
s.d.	3.7	2.2	1.6
Occlusal length	27.1-40.1	31.2-37.2	29.2-34.4
of P^4-M^3	32.7	33.9	32.0
n	36	13	12
s.d.	3.4	2.0	1.5
Alveolar length	28.8-41.7	33.3-40.0	32.0-38.0
of P_4-M_3	35.1	37.3	34.6
n	31	13	12
s.d.	3.6	2.1	1.7
Occlusal length	28.4-40.0	32.9-39.0	32.1-37.5
of P_4-M_3	34.1	36.2	34.1
n	33	14	13
s.d.	3.3	2.0	1.5

they were taken from one specimen.

The basilar length (defined in van Weers, 1976) of the skull (Table 3) differs hardly from the maximum in *H. cristata*. Unfortunately the most important diagnostic character in this subgenus, the 'frontal/nasal ratio' (Corbet & Jones, 1965) could not be measured because some parts are missing and some sutures are fused. The relative length of the nasals of '*H. etrusca*' is smaller than in *H. cristata*, is as large as in the largest *H. indica*, and falls within the range of *H. africaeaustralis*, though below the mean of that species.

The estimated relative width of the nasals falls within the range of *H. indica*, but is above the mean (Table 3). The relative width of the premaxilla process, always negatively correlated with the width of the nasals, is 36 and 43% which falls between the ranges of *H. cristata* and *H. indica*.

The extreme height of the skull in *Hystrix* s.s. is caused by an increase of the length of the nasal bone, accompanied by an inflation of the nasals and frontals. It is indicated by the distance from the palatum to the nasals, is measured at the alveole of the P_4, and expressed as a percentage of the basilar length of the skull (Height/ Bar.l in Table 3). The estimated height (48%) of the Valdarno skulls is larger than the mean relative height in *H. indica* (Table 3).

Table 2. Toothrow measurements in mm of *Hystrix* specimens from Pikermi (Greece), Serrat d'en Vaquer near Perpignan (France), Valdarno Superior and Pirro Nord, Gargano Peninsula (Italy).

Inst. + no.	Locality	Maxill. toothrow		Mand. toothrow	
		Alveol.l.	Occl.l.	Alveol.l.	Occl.l.
UPGM AS II 144	Pikermi	39.3	37.5	-	-
MNLP Pik. 3089	Pikermi	-	-	40.0	42.7
MNLP Pik. 3116	Pikermi	41.0	39.7	-	-
MMPE Pr. 25	Perpignan	-	-	44.5	43.5
MMPE Pr. 147	Perpignan	-	-	47 (est.)	-
DEUF IGF 940	Valdarno	-	-	41.1	39.8
MPVM B	Valdarno	40.3	39.7	-	-
MPVM A	Valdarno	37.0	-	-	-
RGM 263 932	Pirro	-	-	39.8	40.6
RGM 263 934	Pirro	-	-	42.3	-

The conclusion is that the Valdarno skulls are larger than in *H. indica* and possibly larger than in *H. cristata* and *H. africaeaustralis*, that the nasal region is more specialised than in *H. indica* and intermediate between that species on the one side and both *H. cristata* and *H. africaeaustralis* on the other. The dimensions of the teeth (Figs. 1 and 2) do not differ from the topo-typical specimens of *H. refossa*, so *H. etrusca* is considered a junior synonym of that species.

The status of *H. makapensis* Greenwood, 1958 — The material of this species consists of the holotype, a mandibular fragment with a P_4, and a paratype, a mandibule fragment with an M_3, from the '*Australopithecus prometheus*' layer in the Makapan Valley, Transvaal. It was described before (Greenwood, 1955) under the invalid name '*H. major*'. This description is inconclusive concerning the degree of hypsodonty of the teeth, but the mentioned similarity with *H. cristata* and *H. africaeaustralis* makes it probable that its teeth are higher than those of *H. primigenia*. The size of the Makapan porcupine teeth agrees with *H. refossa*, so *H. makapensis* is considered a junior synonym of *H. refossa*.

The status of *H. angressi* Frenkel, 1970 — This species is based on a pair of maxillaries, the holotype, and hundreds of cranial and post-cranial parts from the 'Levalloiso-Mousterian' of the Geula Cave in Israel. The dimensions and morphology agree with *H. refossa*, so this species is listed as a synonym of *refossa*.

The status of the Gombaszög porcupine — Mandible fragments (HNHM V64.1049) and isolated cheek teeth (HGIB, no nrs.) from the Early Pleistocene of Gombaszög, Hungary, are mentioned without specific name by Kretzoi (1938). On the basis of the length of the alveolar toothrow of 39.6 mm, P_4 length 9.6 mm, M_{1-2} length 9.8 mm and the hypsodonty, this material is referred to *H. refossa*.

Other species

Hystrix (Hystrix) primigenia (Wagner, 1848)

Synonyms — *Lamprodon primigenius* Wagner, 1848; *Castor atticus* Roth & Wagner, 1854; *H. bessarabica* Riabinin, 1929; *H. trofimovi* Shevyreva, 1986.

Table 3. Comparison of skull dimensions of '*H. etrusca*' with extant species, with range, mean and number of specimens. Basilar length in mm, and the ratios 'nasal length/basilar length', 'width of nasals/zygomatic breadth', 'width premaxilla process/breadth nasals', and 'height of the skull at P4/basilar length' x 100. The measurements are from adult specimens. Numbers within brackets are ranges after Corbet & Jones (1965).

	'*H. etrusca*'	*H. africae-australis*	*H. cristata*	*H. indica*
Basilar l.	155	129-148	111-156	116-135
mm		139	136	125
n		10	27	8
Nas.l/Bar.l	58	56-62	58-77	49-58
%		60	68	53
n		9	26	7
Nas.b/Zyg.b	60 est.	63-75	61-81	47-64
%		69	71	51
n		9	25	10
P.max/Nas.b	36 and 43	10-18	18-33	50-67
%		(<23)	(19-36)	(>44)
n		9	30	7
Heigt/Bar.l	42>53,	44-54	44-55	39-48
%	48 est.	48	50	44
n		9	30	9

Discussion — Wagner (1848) described an incisor from the Turolian locality Pikermi (Greece, MN zone 12) under the name *Lamprodon primigenius*. Roth & Wagner (1854) published two cheek teeth from the same locality and species under the name *Castor atticus*. Gaudry & Lartet (1856) described a mandible from Pikermi under the name *Hystrix primigenia*, and Wagner (1857) described a skull (UPGM ASII-144) from Pikermi recognizing that all the specimens mentioned above belong to the same species. Depéret (1890) allocated material from Serrat d'en Vacquer near Perpignan to *H. primigenia*, and afterwards specimens from many other Miocene and Early Pliocene localities in Europe followed (Sen & Kovatchev, 1989).

There is considerable confusion about the distinctive characters of this species, such as the shape of the mandible and the cheek teeth, but the only character that holds thus far is the smaller height of the cheek teeth. Masini & Rook (1993) explicitly mentioned that cheek teeth of *H. primigenia* are less hypsodont than in their group of Pleistocene species '*Hystrix* gr. *major-etrusca*' and were the first to give height measurements of cheek teeth. In the diagram of Fig. 2 it is shown that the upper and lower molars from Perpignan have a lesser height than *H. cristata*. No height measurements of isolated cheek teeth were available of specimens from Pikermi. However, in one mandible (UPGM ASII145), roots are visible of some teeth in situ, so the 'crown' height could be estimated. The P_4 of that specimen has a ratio of 'crown' height and length of 0.95 which could be compared with a *H. cristata* specimen (ZMB

70886) with a ratio of 1.55. The relative height of the M_1 in the Pikermi mandible is 0.72, and can be compared with a *H. cristata* (MZVF M4854) and a *H. africaeaustralis* (ZMB 70837) specimen with ratios of 1.16 and 1.42, respectively. So there is no reason to doubt that the specimens from Perpignan belong to *H. primigenia*.

The estimated occipito-nasal length of the damaged Pikermi skull (UPGM ASII-144) is circa 175 mm, which is nearly as large as the largest specimen of *H. cristata* (Table 1). The toothrow lengths (Table 2) of *H. primigenia* from Pikermi and Perpignan are clearly above the means of the extant species (Table 1), as are the isolated teeth of *H. primigenia* (Fig. 1). Table 2 shows that the dentitions of *H. refossa* from Valdarno and Pirro are of about the same size as those of *H. primigenia*.

The status of *H. bessarabica* Riabinin, 1929 — The holotype of this species, a part of a skull with most of the cheek teeth, from the Late Miocene of Taraklia, Bessarabia, could not be studied. The specimen cannot be identified on the basis of the information available. It may represent *H. primigenia*.

The status of *H. trofimovi* Shevyreva, 1986 — The holotype is a fragment of a maxillary with P^4-M^2 from the Upper Pliocene of Tadjikistan. The figure in the original description and a photograph (Nikiforowa & Wangengeim, 1988) of the very low-crowned paratype P_4, provide an argument for the synonymy of that species with *H. primigenia*. This implies an extension of the stratigraphic range of this species.

The status of the Polgárdi porcupine — Kormos (1911) mentioned 7 cheek teeth from the Late Miocene (MN zone 13) of Polgárdi, Hungary, with the name '*Hystrix* cf. *primigenia*'. All these teeth (HGIB Ob4619) are clearly brachyodont (or 'moderately hypsodont') and agree in this respect with *H. primigenia*. An M^{1-2} and an M^3 have an occlusal length of 8.4 mm which is rather small for this species. Three lower cheek teeth with lengths of 10.1 to 11.9 mm agree in size with *H. primigenia*, but two of these have extremely complicated enamel structures for this species. Two not yet fully developed specimens cannot be interpreted. Kormos's (1911) allocation is therefore followed.

Subgenus *Acanthion* F. Cuvier, 1823

Hystrix (*Acanthion*) *vinogradovi* Argyropulo, 1941

Synonyms — *H. schaubi* Brunner, 1954; *H. cristata minor* Malez, 1963; *H. vinogradovi atavus* Jánossy, 1972; *H. vinogradovi kudarensis* Baryshnikov & Baranova, 1982.

Discussion — This species is based on a number of maxillary and mandible remains from the Middle Pleistocene of Binagady, Apsheronskiy Peninsula, easternmost Caucasus and is distinguished on its small size. Gromov (1952) mentioned a length of 28.5 mm of one upper toothrow, and in 6 lower toothrows a mean of 29.7 mm. Baryshnikov & Baranova (1982) mentioned a range of 28.4-30.7 mm (mean 29.3 mm) from a sample of 11 D_4-M_3 toothrows, for two P_4-M_3 tooth series a length of 28 mm, of two isolated M^{1-2} teeth lengths of 6.6 and 6.7 mm, and for a sample of 12 M_{1-2} teeth the range 6.9-8.5 mm (mean 7.5 mm). Comparison of these dimensions with our Fig. 1 and Table 2 shows that we certainly are dealing with a smaller species than *H. refossa*. Jánossy (1972) demonstrated that these two species occurred together in the Early Pleistocene of Osztramos-8 (Figs. 1-2).

As will be discussed below, *H. vinogradovi* may be closely related to the Southeast Asian *Hystrix (Acanthion) brachyura* Linnaeus, 1758. As mainly teeth and no cranial parts are available, no proof exists that they are conspecific, so provisonally the name *H. vinogradovi* will be maintained.

The status of *H. schaubi* Brunner, 1954 — This species was distinguished on the basis of a detail in the occlusal surface of the P_4 in a fragment of a mandible with P_4-M_2, UPGM 6558, from the Late Pleistocene of the Fuchsloch Cave, Bavaria, Germany. Measurements of the holotype fit the dimensions of *H. vinogradovi,* and the morphology of the occlusal pattern does not show significant differences. This species is therefore considered a junior synonym of the latter species.

The status of *H. cristata minor* Malez, 1963 — No specimens could be studied of the Late Pleistocene cranial and post-cranial material from the Veternica Cave, Medvednica, Croatia. The alveolar length of a P_4-M_3 of 30.5 mm is not different from the measurements available for *H. vinogradovi,* so Malez' species is considered a junior synonym of the latter.

The status of *H. vinogradovi atavus* Janossy, 1972 — Two mandible fragments, among which the holotype HNHM V72.02, and some isolated teeth and postcranial parts from the Early Pleistocene of Osztramos-8, form the hypodigm of this subspecies. It has been distinguished by the slightly smaller toothrow (alveolar length 27.2 mm) of the type and the somewhat different shape of two D_4. However, these minor differences in such a small sample do not justify subspecific distinction.

The status of *H. vinogradovi kudarensis* Baryshnikov & Baranova, 1982 — This subspecies is based on the occlusal pattern in the M_2 and M_3 of a mandible fragment from the Late Pleistocene of a cave near Kudaro, Transcaucasus. However, occlusal patterns are variable in this genus and do not allow taxonomical differentiation of a single specimen.

Inadequately or doubtfully allocated specimens — Two mandible fragments (HGIB Ob.4608) from Brassó, S.E. Rumania of Early Pleistocene age are labelled '*Hystrix hirsutirostris*', which is a junior synonym of *H. indica* Kerr, 1792. The length of the M_1 is 8.8 mm; this is somewhat large for *H. vinogradovi* and falls within the range of *H. indica* (7.4-9.3 mm, mean 8.5 mm, n = 22) in my files. However, when large samples of these species will become available an overlap in size may be expected. Therefore their attribution to *H. vinogradovi* is most probable.

A mandible fragment (NMP 28.057) with P_4-M_2 from a cave at Ostrov near Macocha, Moravia, 'Pleistocene', was labelled '*H. leucura*', which is a junior synonym of *H. indica.* The length of the teeth, 8.1, 7.1 and 7.6 mm respectively, is nearly the same as in the smallest specimens of *H. indica,* but their attribution to *H. vinogradovi* is more likely on these dimensions.

Three mandible fragments and some postcranial parts (HNHM, no nrs.) from the Kiskevélyi Cave, Csobánka, Hungary, Late Pleistocene, are also labelled *H. hirsutirostris.* On the basis of the length of a toothrow (alveolar 29.5 mm) they are allocated to *H. vinogradovi.*

A mandible fragment (HNHM V60/715) from the Köháti Cave, Bükk Plateau, Hungary, of Late Pleistocene age with an alveolar toothrow length of 29.8 mm is clearly referable to *H. vinogradovi.*

A mandible fragment (HNHM V.62.426) from the Lambrecht Cave, Varbó, Hungary, Late Pleistocene, with P_4-M_2 with occlusal lengths of 7.2, 7.3 and 7.8 mm respectively, is considered to belong to *H. vinogradovi*.

One M^1 and one M^2 (NMP CN439) from Podbaba, Kotlárka, Czech Republic, of uncertain age are figured by Kafka (1892) and identified as '*Hystrix hirsutirostris* ?'. The largest of these two teeth has a width of 6.7 mm and a length of 6.3 mm, so this specimen is referred to *H. vinogradovi*.

Remarks

The subgeneric assignation of the fossil *Hystrix* species — The three largest extant porcupine species, with enlarged and inflated nasal bones from Africa and S.W. Asia, are united in the subgenus *Hystrix*. The subgenus *Acanthion* Cuvier, 1823 contains two, on the average smaller species (van Weers, 1979) from S.E. Asia. These have relatively smaller and less inflated nasal bones. There is considerable overlap in cranial characters between these subgenera; externally a clear distinction is possible on the basis of the different colour distribution on the large spines. The porcupine of the subgenus *Acanthion* which differs least from *Hystrix* s.s. is *H. brachyura subcristata* Swinhoe, 1870. Comparison of the alveolar toothrow lengths of that subspecies, P^4-M^3 = 25.3-31.8 mm (mean 29.1 mm, n = 22) and P_4-M_3 = 26.4-33.7 mm (mean 30.3 mm, n = 23) with those of *H. indica* in Table 1, shows an overlap in size.

H. primigenia is generally allocated to *Hystrix* s.s. because it is large. The only skull available (UPGM ASII144) is strongly distorted and incomplete but suggests the specialisations of the subgenus. The *H. refossa* skulls from Valdarno clearly show that this species fits in *Hystrix* s.s. too.

No skull of *H. vinogradovi* is available, so its subgeneric attribution is less clear. Brunner (1954) mentioned the similarity of his *H. schaubi* with *H. brachyura* from Sumatra, but was misled by an unimportant, aberrant detail in the enamel pattern of the P_4 of his holotype. Jánossy (1961, 1964) discussed and rejected a close relationship of *H. vinogradovi* with the S.E. Asiatic species as well, but that opinion was based on scarce comparative material. This was probably also the reason for Malez's (1963) classification of his *H. vinogradovi* specimens as a subspecies of *H. cristata*. However, the measurements of *H. vinogradovi* quoted before, perfectly fit those of *H. (Acanthion) brachyura* in van Weers (1979, 1990). Since other diagnostic characters are not yet known, a close relationship of *H. vinogradovi* with the species of the Southeast Asiatic subgenus *Acanthion* is probable.

Relation of hypsodonty with mandible height — Sen (1994) expressed the height of the mandible between the P_4 and M_1 as a percentage of the length of the toothrow, supposing that there is a correlation of the height of the mandible and the height of the cheek teeth. They found 56.3% for a Pikermi, 61.3% for a Perpignan specimen and a mean of 78.5% for ten *H. cristata* specimens. Measurements from our photograph of one of the mandibles from Pikermi (MNLP 3089) yield a ratio of 62.5%, so not very different from Sen's observations. From 8 African *Hystrix cristata* and *H. africaeaustralis* specimens (ZMA) a mean of 71% (range 64-75%) was measured, so the difference with *H. primigenia* is clearly smaller than is shown in the data above. Measurements of two *H. refossa* specimens (RGM 263 932 and 263 934) from Pirro, a locality first mentioned by Freudenthal (1971), show percentages of 61 and 73%. In 10 specimens of *H. brachyura* Linnaeus, 1758 from Sumatra (ZMA) a mean value of 77% was found (range 63-100%). This ratio is possibly also related to absolute size, with a more robust size in smaller species, and a more slender shape in larger ones. In any case a considerable overlap exists in this character and only the means of large samples allow conclusions.

The shape of the cheek teeth in H. refossa and H. primigenia — Koliadimou & Koufos (1991) observed a more elongated shape of the occlusal surface in the cheek teeth of their *H. refossa* specimens from Gerakou, Macedonia, than in *H. primigenia*. They expressed this in the ratio 'occlusal width/occlusal length' and used the term 'robusticity index'. This character was studied for comparison in 94 M^{1-2} teeth of *H. cristata* in my files, subdivided in wear classes and here expressed as a percentage. The classes A and B (not fully grown) and H (totally worn) are not considered.

The width as a percentage of the length in this sample is:

class C-E	60-92%	mean 82%	n = 28
class F	80-99%	mean 90%	n = 27
class G	83-146%	mean 105%	n = 39.

All our fossil M^{1-2} teeth studied of *H. refossa* and *H. primigenia*, their wear classes taken into account, fall within the given ranges. In our total sample of *H. cristata* M_{1-2} (n = 99), from wear class O (scarcely worn) to class T (highly worn), this ratio varies from 57 to 108% (mean 81%). All specimens of the two fossil species measured fall within this range. In the light of the variability and the effect of attrition, differences between small samples are insignificant.

The occlusal pattern — Sulimski (1960) mentioned a maximum number of 6 islands in lower molars of living species against 8 in *H. primigenia*. Sen & Kovatchev (1987) stated that *H. indica* and *H. cristata* have a dental pattern with fewer enamel islands than fossil *H. primigenia*, giving a nummber of 4 to 7 islands for the upper cheek teeth of the Bulgarian *H. primigenia* they described. However, Frenkel (1970) figured an M_3 of *H. indica* with 9 enamel islands, and van Weers (1993) figured a P^4 of *H. cristata* with 8 islands, thus illustrating that these morphological characters are inconclusive when small samples are available.

Conclusions

The topotypes of *H. refossa* Gervais, 1852 from the Bravard collection in the British Museum (Natural History) show that there is no difference in size between this species and *H. major*. As a consequence the latter species is a junior synonym of *H. refossa*. The type material of *H. major* Gervais, 1859 is lost.

The main difference between *H. refossa* and *H. primigenia* is primarily the lesser hypsodonty of the cheek teeth of the latter species.

H. refossa occurs from the Late Pliocene (MN 16, Etouaires, France) to the Late Pleistocene (Geula Cave, Israel).

H. vinogradovi Argyropulo, 1941 (= *H. schaubi, H. cristata minor, H. v. atavus and H. v. kudarensis*), ranges from the Early to the Late Pleistocene.

On the basis of the fossil material, mainly teeth, *H. vinogradovi* Argyropulo, 1941 cannot be distinguished from the extant *H. brachyura* Linnaeus, 1758. But because in this genus teeth alone are not conclusive, the distinction is maintained.

H. indica Kerr, 1792 may have occurred in the Pleistocene of Europe, but by an overlap in the range of its dimensions with *H. refossa* as well as with *H. vinogradovi,* remains cannot be identified with certainty.

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