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First discovery of *Hystrix primigenia* WAGNER from the Late Miocene to Early Pliocene deposits of Shahinova, Berat, South-West Albania.

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Abstract

A hystricid fragment of left hemimandible L.P.H. 85/7 with I_1, M_2-M_3 is described. The specimen has been discovered in the fossiliferous quarry of Shahinova, Ura Vajgurore, Berat County, south-west Albania, in the Balkan Peninsula. It is part of a fossil sample of small and large mammals which is under study. The large mammals sample includes also scarce remains of *Protoryx* sensu lato recovered from the same levels. Morphological and metric comparisons of L.P.H. 85/7 with *Hystrix primigenia* WAGNER, from Pikermi and other Neogene deposits from the Balkan Peninsula and other parts of Europe, support the taxonomic assignment of this specimen to *Hystrix primigenia*. It belongs to a large size porcupine, twice the size of the Pleistocene *Hystrix*. The Shahinova lowermost levels are dated to Late Miocene/Early Pliocene age. The material is similar to that recovered from Turolian levels of the Mediterranean sites of Pikermi, Samos (Greece) and Kemiklitepe (Turkey).

The southern European areas of the Balkan peninsula and Asia Minor are central to *Hystrix* radiation and dispersal during the Late Miocene. Aspects of taxonomy, paleoecology and morphology of the genus *Hystrix* in Europe are discussed.

Zusammenfassung

Ein Fragment einer linken Mandibel L.P.H. 85/7 mit I_1, M_2-M_3 eines Hystriciden wird beschrieben und ist Teil einer Groß- und Kleinsäugerfauna, die derzeit bearbeitet wird. Das Stück wurde in einer fossilführenden Spalte von Shahinova, Ura Vajgurore, Kreis Berat, Südwest- Albanien, Balkan-Halbinsel, entdeckt. In denselben Lagen fanden sich neben Großsäugetieren wenige Reste von *Protoryx* s.l. Morphologische und metrische Vergleiche von L.P.H. 85/7 mit *Hystrix primigenia* WAGNER aus Pikermi und anderen Neogenfundstellen der Balkan-Halbinsel und anderer Regionen Europas unterstützen die taxonomische Zugehörigkeit zu *Hystrix primigenia*. Es ist ein großwüchsiges Stachelschwein, zweimal so groß wie das pleistozäne *Hystrix*. Das Alter der tiefsten Lagen von Shaninova ist Obermiozän/Unterpliozän. Das Material ist jenem aus den mediterranen Lokalitäten Pikermi, Samos (Griechenland) und Kemiklitepe (Türkei) ähnlich.

Zentrum der Radiation und Verbreitung von *Hystrix* im Obermiozän sind die südeuropäischen Regionen, die Balkan-HAlbinsel und Kleinasien.

Taxonomie, Palökologie und Morphologie der Gattung *Hystrix* werden diskutiert.

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Introduction

Geological information about Neogene deposits in Albania has recently been reported, and their location has been established (SHKUPI 1992). Recently, vertebrate fossil material has also been reported from Neogene deposits of Albania (FISTANI 1994). Other mammalian fossil remains of Late Miocene - Early Pliocene age as well as of Early Pleistocene age (Villafranchian) have been recovered from South-East and South-West Albania. They are presently under study (FISTANI & al., in prep.).

The Balkan region constitutes a geological and palaeofaunal continuum. The vertebrate fauna recovered recently in Albania is considered part of the southern European Neogene mammalian biogeographic regime (sensu PAVLAKIS 1987; BERNOR & PAVLAKIS 1987). The Thessalian-Albanian depression in eastern Albania displays the same geological characteristics as in its southern exposure in Greece, and contains a large mammal fossil fauna.

The fossil material presented here was discovered by the first author during the summer of 1985 in the lowermost levels of a fossiliferous red clay and karst network of deposits in the Shahinova quarry near the town of Berat, in southern Albania (Figure 1). The fossil sample includes both large and small mammals. Here, the micromammal material is reported.

The stratigraphic section of Shahinova is 16 to 18 m long. It is probably part of the Periadriatic depression, where Messinian and older deposits extend below a transgressive Pliocene Formation. Lithologically, the geological formation consists of large size calcareous blocks, conglomerates and cement gravels mixed with red clay sediments. Percolating water created interstices and vertical openings. The Shahinova quarry revealed also an old karst with red clay fissure fillings. In several levels, the clay sediments are cemented and include also calcareous blocks and various conglomerates. The cemented clays contained the fossil bone fragments. The depositional environment indicates drastic climatic changes occurring during a temperate transitional rainy period. The fossil material recovered in Shahinova indicates two different faunas. The one recovered from the upper level is a faunal sample of Pleistocene age which contains mostly Cervids, Ursids and *Rhinoceros*. The fauna recovered from the lowermost levels, contains elements of Late Miocene to Early Pliocene age. It is represented by less material than in the upper levels. These include remains of *Hystrix primigenia*, *Protoryx* as well as a small sample of additional rodent microfauna. The material was recovered by the first author and it is housed in the collections of the Laboratory of Human Palaeontology and Prehistory, University of Shkoder "Luigj Gurakuqi" in Shkoder, Albania (LHP).

The first report of *Hystrix* in Albania (*Hystrix* cf. *vinogradovi* ARGYROPULUS) is in the Mid-Pleistocene fauna of Gajtan 1 (FISTANI 1993). Here, the material of *Hystrix primigenia* WAGNER, from Shahinova, Berat is reported and described. The study was conducted in the Laboratory of Human Palaeontology and Prehistory, University of Shkoder "Luigj Gurakuqi" in Shkoder, Albania, in the Museum of Palaeontology of the Department of Geology, University of Athens, Greece, in the Vertebrate Palaeontology Laboratory, University of Texas, in Austin, USA, and the International Institute for Human Evolutionary Research in Oregon, USA. The fossil material is compared with other Hystricinae specimens of Late Miocene age from Pikermi, Greece; with Middle

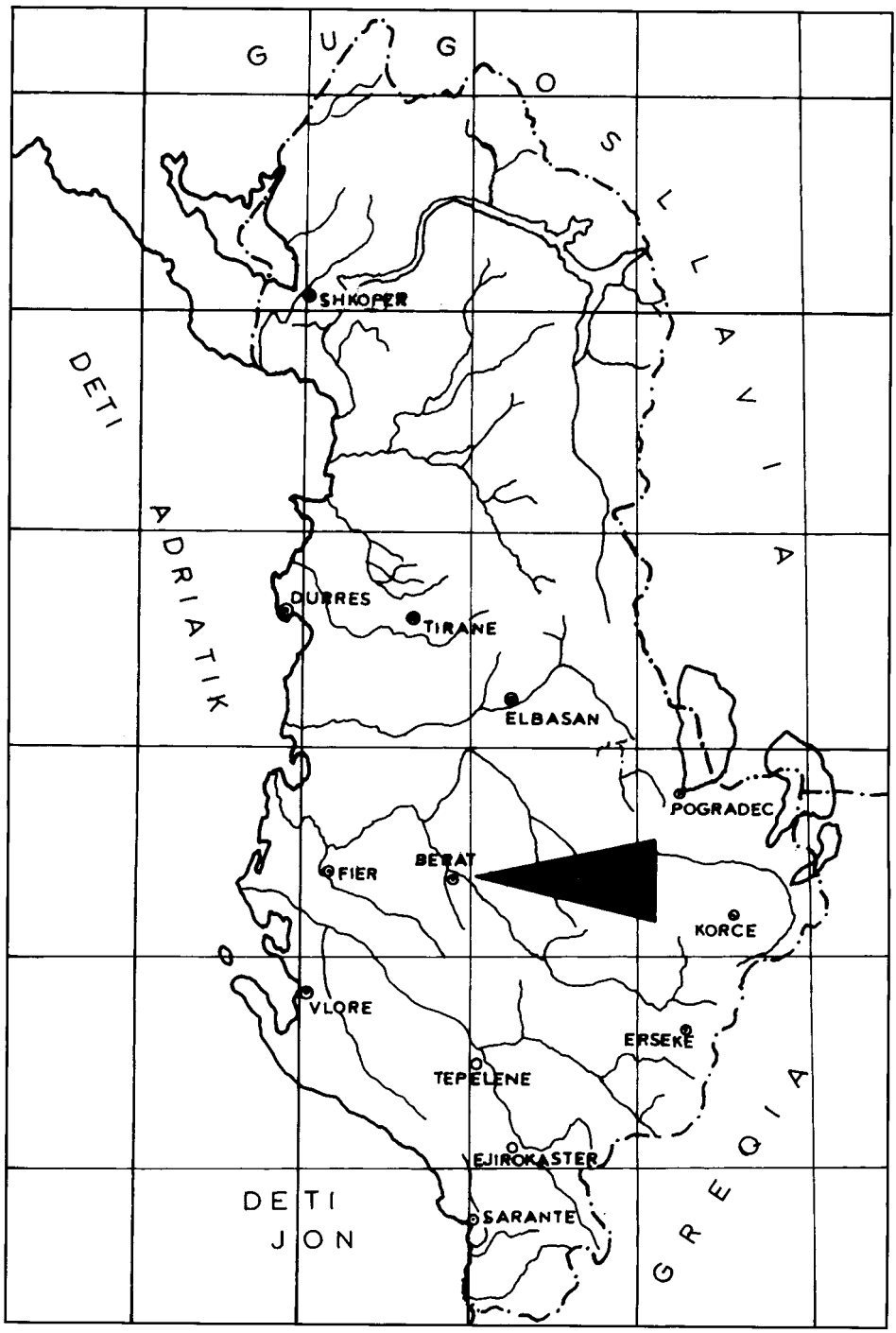


Figure 1. Map of Albania. The arrow indicates the city of Berat, which is located near the Shahinova site. This area is close to the Albanian-Thessalian Depression.

Pleistocene specimens of *Hystrix* cf. *vinogradovi* from Gajtan 1, Albania; with *Hystrix* material recovered at Repolusthöhle cave in Graz, Austria, with specimens of American species of porcupine housed in the Vertebrate Palaeontology Laboratory in the University of Texas and with other specimens from the Museum of Palaeontology in the University of Athens, as referenced in the tables. Further comparisons were made possible from the literature.

Systematic Description

Order Rodentia BODWICH, 1821

Family Hystricidae BURNETT, 1830

Subfamily Hystricinae LYON, 1907

Genus *Hystrix* LINNAEUS, 1758

***Hystrix primigenia* WAGNER, 1848**

L o c a l i t y: Shahinova, Ura Vajgurore, Berat, Southwest Albania.

A g e: Late Miocene – Early Pliocene.

M a t e r i a l: L.H.P. 85/7 Left Hemimandible ramus with I_1, M_1 alveolus, M_2, and M_3.

D e s c r i p t i o n a n d C o m p a r i s o n

A left mandibular fragment with an almost complete alveolar portion of I_1 remaining, P_4 missing, M_1 alveolus in place, and complete M_2 and M_3 teeth presenting full wear (Figure, 2). The hemimandible is broken and the incisor root can be seen into the alveolus. The tooth was fragmented in several places and was reconstructed by the first author. Microscopic observation of M_1 alveolus shows divergent roots, a primitive hystricid characteristic. The M_1 must have had an almost quadrangular outline as witnessed by the present clay sediment cast of the M_1 area which preserves the tooth morphology at the time of death. In general the remaining lower teeth present subequal occlusal surface shape, with the antero-posterior diameter being slightly greater than the transverse. The mandibular diastema although fragmented in the Albanian specimen does not display a strong degree of curvature. The mandibular body is larger and more elongated than in the living *Hystrix cristata* as well as in the Middle Pleistocene *Hystrix* cf. *vinogradovi* from Gajtan 1. This feature is also observed in mandibles of *Hystrix primigenia* from Pikermi. The missing areas of both pars alveolaris and pars incisivum in our specimen make difficult accurate comparisons of this taxonomically important anatomical region with other porcupine records. We can deduce, however, that in the L.H.P. 85/7 specimen the pars alveolaris and pars incisivum were at the same level and that the mandibular curvature was not very deep. The ramus mandibularis is missing.

I_1: The incisor is large. It is broken transversally at two different levels. Additional fissures are also visible in the enamel surface. Postmortem damage was produced at the half symphysis level of the hemimandible, fragmenting the incisor as well. This apparently enlarged the diameter of the tooth. It seems that the tooth has been more circular in diameter in the original curvature, and was positioned closer to the mid-line of the

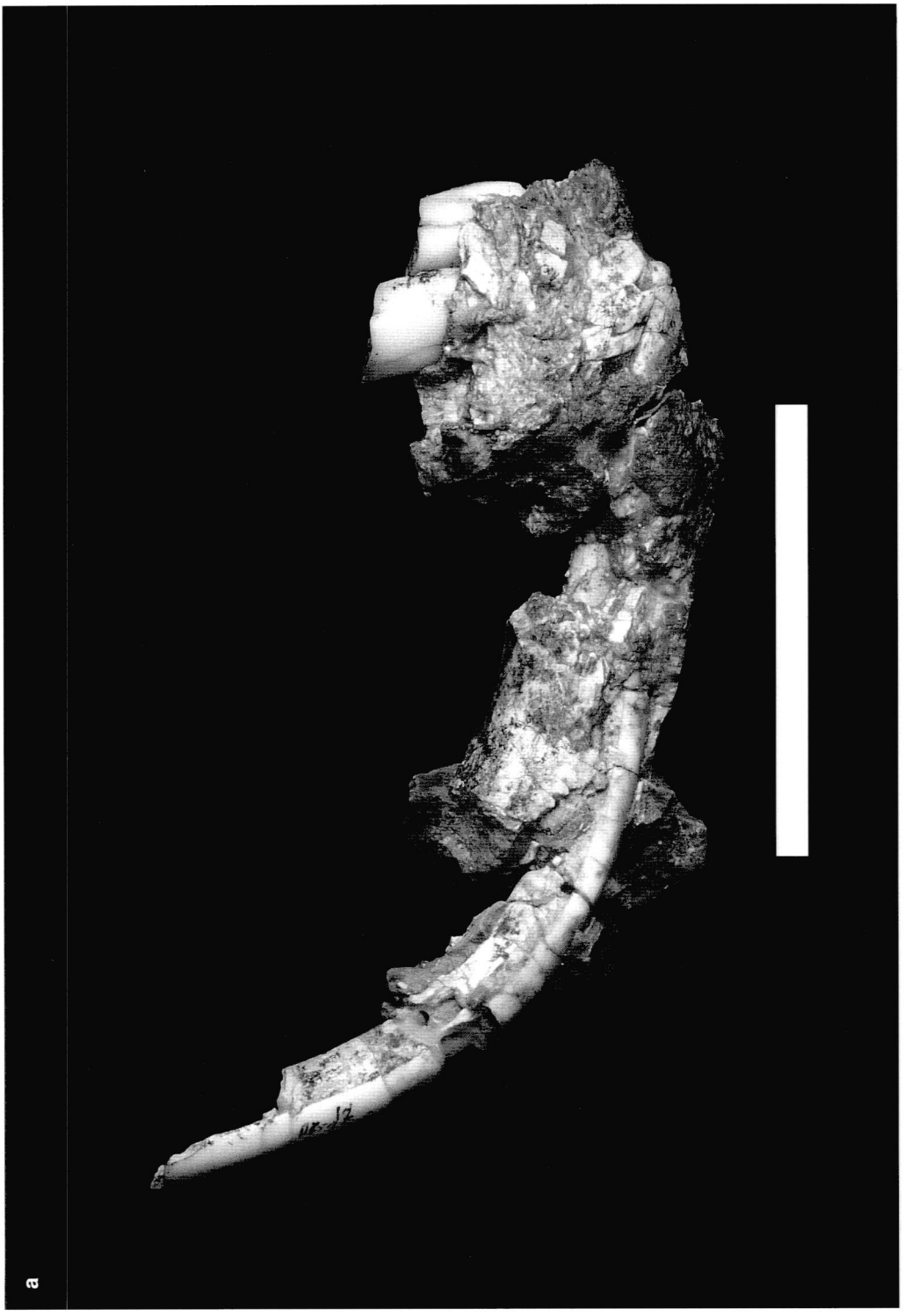
tooth raw. The cross section of the *H. primigenia* incisor from Albania is semicircular anteriorly and almost subtriangular posteriorly. This feature is encountered in *H. primigenia* specimens from Pikermi, Greece (GAUDRY 1862-1867) and from Kalimanci, Bulgaria (SEN & al. 1987). The incisor enamel displays a characteristic yellowish pigmentation anteriorly, and a dark grey colour posteriorly. This coloration pattern is also reported in the incisors of *H. primigenia* from Pikermi (GAUDRY 1862-1867), from Macedonia, Greece (De BONIS & al. 1992), as well as from Weze, Poland (SULIMSKI 1960). The enamel on the anterior aspect of I_1 in the specimen L.H.P. 85/7 from Albania, is well developed and covers the anterior one third of the tooth surface.

Although *Hystrix primigenia* was erected based on lower incisor teeth from Pikermi, further discoveries did not bring to light additional specimens of I_1. Actually lower incisor data are generally scarce for *H. primigenia*. GREENWOOD (1955) reported some *H. primigenia* mandibular teeth measurements, including those of lower incisors. *H. primigenia* I_1 from Pikermi measured 8.5 mm in its maximum anteroposterior diameter. The specimen from Albania displays almost the same dimensions (L=8.4 mm). The L.H.P. 85/7 specimen, therefore, belongs to a *Hystrix* of comparable size to that from Pikermi. SEN (1994) also reports a lower incisor from Kemiklitepe, Turkey, which has larger dimensions than the specimens from both Shahinova and Pikermi (Table 1). Porcupines have one pair of incisors, so the upper and lower do not present significant difference in size and in robustness (WAHLERT 1968). In table 1, we compare the lower incisor's measurements of *Hystrix primigenia* from various localities with the Albanian fossil. We included also upper incisors in the comparison. The index of robustness, as well as their morphology are similar to L.H.P. 85/7 lower tooth from Shahinova.

LOWER INCISORS	L	B	IR
H. primigenia, Shahinova	8.4 mm	6.4 mm	76.1
H. primigenia, Pikermi (GREENWOOD 1955)	8.5 mm	-	-
H. primigenia, Kemiklitepe (SEN 1994)	9.7 mm	7.2 mm	85.7
UPPER INCISORS			
H. primigenia, PMNH, PIK-3191 Pikermi, (De BONIS & al., 1992)	8.0 mm	6.1 mm	76.2
H. primigenia, Weze, (SULIMSKI 1960)	8.5 mm	6.5 mm	76.4

Table 1: Measurements of *Hystrix primigenia* upper and lower incisors from various localities compared with specimen L.P.H. 85/7 from Shahinova, Albania. L = maximum antero-posterior diameter. B = maximum bucco-lingual diameter. IR = Index of robusticity or shape, I.R= B/L x100.

M_2: The main characteristic of the molar tooth seen in occlusal view, is its subtriangular shape and the thick enamel borders. A unique morphological pattern is the presence of a large fold located in the vestibular side, and continuing down the wall border. The absence of other such folds indicates an advanced stage of wear and a tooth belonging possibly to an old individual. The anterolophid and the protoconid are united, and only the hypoconid is divided by a vestibular sinclinal. A large posterolophid area shows an almost transversal islet. At the level of mesolophid, the tooth displays an evident concavity situated in the lingual aspect of the tooth. The occlusal surface shows five islets.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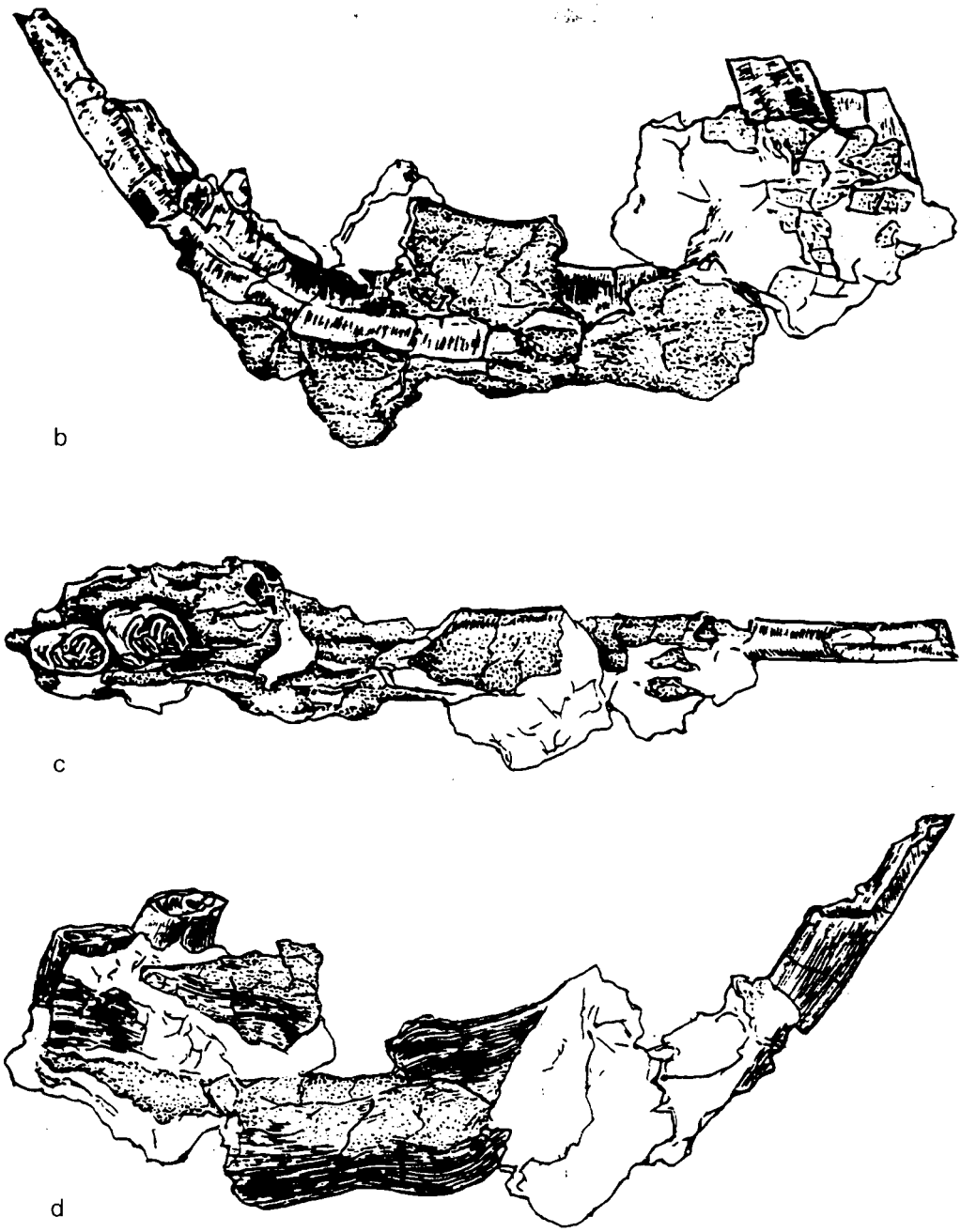

Figure 2. *Hystrix primigenia* WAGNER, LPH 85/7, left hemimandibule fragment from the lowermost levels of Shahinova quarry, Ura Vajgurore, Berat, South-West Albania;

a in vestibular view, scale = 5 cm;
b in vestibular view, x 1,18;
c the same in occlusal view, x 1,18;
d the same in lingual view, x 1,18.

The morphology of the second molar of the L.H.P. 85/7 hemimandible shows similarities with the homologous tooth from Kalimanci, Bulgaria (SEN & al. 1987), and from Monticino, Italy (MASINI & al. 1993). The M_2 from Shahinova presents intermediate amount of wear between the two *H. primigenia* specimens from Bulgaria ("adult old" and "old" individuals, SEN & al. 1987). The specimen from Monticino shows a slightly more advanced wear pattern. We believe that the tendency of porcupine molars towards a quadrangularly shaped cross section, depends on the degree of wear. This is supported by the shape of the molar cross section and the degree of wear of the Albanian fossil. The specimen from Weze, an "old" individual, displays a more rounded cross section shape than the molar of L.H.P. 85/7 from Shahinova.

Based on the dimensions of the M_2 (L=11.4 mm, W=9.5 mm, Table 2), the specimen L.H.P. 85/7 enters into the metric values range of *Hystrix primigenia* from Pikermi, Kalimanci, Weze and Monticino. A notable size difference is encountered between our specimen and that of the Middle Pleistocene *Hystrix* cf. *vinogradovi* from Gajtan 1, Albania, which is much smaller (see Table 2).

M_3: The tooth displays the general *Hystrix* morphology. The posterolophid is smaller than the anterolophid, as is typically the case with *Hystrix* M_3's. This feature, furthermore, contrasts with the occlusal morphology of the M_2. The tooth is situated in a lower level than the estimated for the M_1, probably due to a postmortem deformation. The anterior occlusal part presents an anterolophid which consists of the protoconid and the metaconid. It has an almost rectangular shape, which is different from the more rounded typical occlusal morphology of the anterior part of M_3 in *Hystrix*. In L.H.P. 85/7, the M_3 has a subtriangular occlusal shape. This feature is also presented by the Monticino specimen of *H. primigenia*. A sinclinal at the vestibular aspect, forms a fold between the hypoconid and protoconid. Seen in occlusal view the tooth displays six islets situated transversally. This important characteristic of *H. primigenia* third molar has been underlined by DÉPERET (1890) when he described the porcupines recovered from the Roussillion site in France. Metric data of the Albanian specimen corroborate with comparable records of *H. primigenia* from Pikermi, Kalimanci, Weze and Monticino (Table 2).

Discussion

Pikermi, Greece is the type locality of *Hystrix primigenia* WAGNER. The taxon includes *Lambrodon primigenia* WAGNER (1848) and *Castor atticus* ROTH & WAGNER (1854). GAUDRY & LARTET (1856) named it *Hystrix primigenia* (keeping in his honor the name of first describer- WAGNER). Although many specimens have been recovered since then, the complete paratype is still not sufficient to fully reconstruct its phylogenetic relationships (WOOD 1950, 1974, 1985). Recent discoveries include a skull from Macedonia, Greece (de BONIS & al. 1992), a small fossil sample from Kalimanci level IV, Bulgaria (SEN & al. 1987), and the material from Kemiklitepe (SEN 1994) and from Dardanelles, Turkey (UNAY & al. 1984). They contributed to the better knowledge of this taxon, especially from the Balkan peninsula, since they increased the fossil sample already known from Pikermi, and Umen Dol, ex-Yugoslavia (GAREVSKI 1956). Other localities in Europe that yielded porcupine specimens of Neogene age include: Monticino, Italy (MASINI & al. 1993); Roussillon, France (DÉPERET 1890); Villaroya, Spain (AGUSTI & al. 1987), and Weze, Poland (SULIMSKI 1960).

HYSTRICID SPECIMENS		P_4	M_1	M_2	M_3
H. primigenia, Shahinova	L	-	10.1*	11.2	10.2
	B	-	9.1*	9.5	8.0
	IR	-	90.0	84.8	78.4
H. primigenia, Pikermi	L	12.0	10.5	11.0	10.3
	B	11.0	11.0	11.0	9.0
	IR	91.6	104.7	100.0	87.3
H. primigenia, Halmyropotamos (2,67/11.12)	L	-	-	9.5	9.3
	B	-	-	- 8.6	7.9
	IR	-	-	90.5	84.9
H. primigenia, Monticino 1	L	12.3	10.8	11.0	10.4
	B	10.6	9.9	10.8	9.6
	IR	86.1	91.6	98.1	92.3
H. primigenia, Kalimanci, L-IV	L	10.7	10.8	11.4	10.2
	B	9.3	9.6	9.3	8.3
	IR	86.9	88.8	81.5	81.3
H. primigenia, Weze	L	12.4	11.7	11.7	10.0
	B	9.7	11.2	11.2	9.7
	IR	78.2	95.7	95.7	97.0
H. cf. *vinogradovi*, Gajtan 1	L	7.5	7.2	7.7	-
	B	5.8	5.8	6.3	-
	IR	77.3	80.5	81.8	-
H. cf. *indica*, Kerr (Leiden Museum)	L	9.0	8.9	10.1	9.0
	B	7.4	7.0	7.8	7.5
	IR	79.5	78.6	77.2	83.3
H. cristata, (recent, means)	L	9.1	8.1	9.3	8.8
	B	7.5	7.5	8.6	8.2
	IR	81.9	92.0	92.5	93.2
H. cristata, (N. Africa, GREENWOOD 1955)	L	10.5	8.5	9.0	8.5
	B	7.7	7.0	7.7	7.5
	IR	73.8	82.3	86.1	88.2

Table 2: Comparison of postincisive teeth measurements of *Hystrix primigenia* L.H.P. 85/7 from Shahinova, Albania, with hystricid specimens from Pikermi, Greece (GAUDRY, 1862-67), Halmyropotamos, Greece (MELENTIS 1967), Kalimanci, Bulgaria (SEN & al., 1987), Monticino, Italy (MASINI & al. 1993), Weze, Poland (SULIMSKI 1960), and *H.* cf. *vinogradovi* from Albania, (FISTANI 1993), *H.* cf. *indica* (HOOIJER 1961) and recent *H. cristata*. (Measurements in mm. I.R. as for Table 1. * Measurements into alveolus)

This report, of *Hystrix primigenia* recovery for the first time from the Periadriatic region of Albania, in addition to numerous other discoveries made over the years, (especially those made recently from South Europe and Asia Minor), stress the significance of the Balkan region for understanding the evolutionary history of porcupines during the Late Miocene. The fossil record of *Hystrix* in the Balkans, argues that large populations of hystricids moved into South Europe during Late Miocene. They adapted to the environment, radiated and dispersed from there.

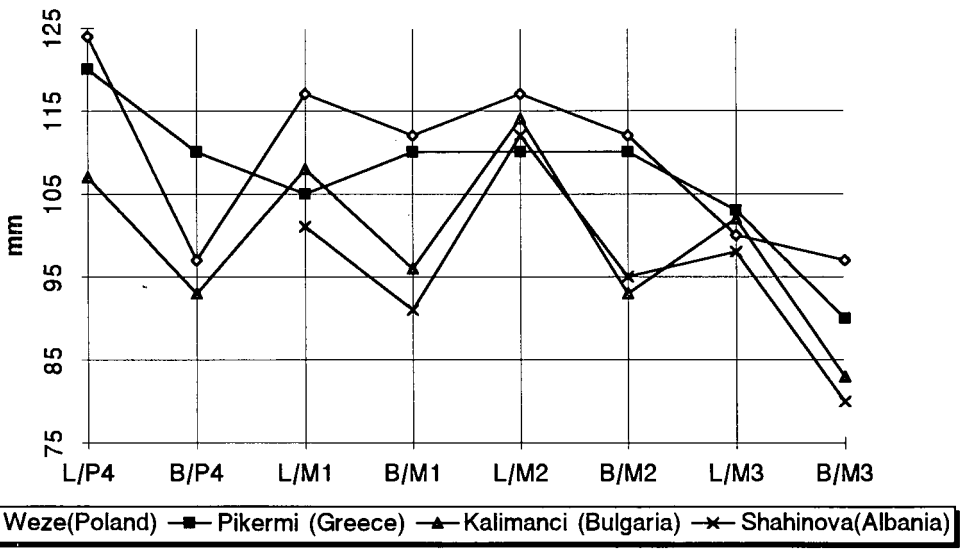

Figure 3. Diagram of lower postincisive teeth dimensions (in mm) of *Hystrix primigenia* from different European sites, compared with the Shahinova specimen (Data and references in Table 2).

One of the vexing problems of the family Hystricidae is, that the species included lack sound differentiating morphological criteria. Perhaps this is related to the frequent change of their tooth morphology caused by constant wear during the animal's life. In addition, the scarcity of fossil material combined with the lack of studies on hystricid postcrania created a hiatus in our knowledge of the phylogenetic relationships of this taxon. The determination of the stage of wear seems to be an important step towards a more accurate study and comparison of fossil hystricids. The hypothetical scale of tooth wear stages proposed by SULIMSKI (1960), seems to be significant in this respect. In addition, MOTTL (1967) draws attention to certain anatomical criteria concerning the structure of the mandible of Pleistocene *Hystrix*, which can be of phylogenetic value. If some minor morphological differences, however, are detectable between Mio-Pliocene and Pleistocene species of *Hystrix*, the metric differences are quite evident. The Mio-Pliocene group of species consists of the large sized porcupines, while the Pleistocene age group consists of the small size *Hystrix cristata* and its allied species.

The metrical comparison of the hemimandible L.P.H 85/7 with other European hystricid specimens, including with samples from adjacent Greece and Bulgaria, is presented in the figures 3-6. These comparisons, as well as the morphology of the occlusal surface (in figure 7) support the taxonomic classification of the hemimandible from Shahinova, Albania, into *Hystrix primigenia*. Metric comparison of *H. primigenia* lower postincisive teeth length and width dimensions discovered in a number of sites is presented in figure 3. In figure 4, the same dimensions are presented as percentage of the *H. primigenia* from Pikermi, which was taken as 100%. Both show that the Shahinova porcupine and that from Kalimanci are closer in size, while the *H. primigenia* from Weze (Poland; Figs 3,4), as well as the recent *H. cristata* (Fig. 4) are much different. Furhtermore, we have considered the index of robusticity (I.R.) or the index of surface

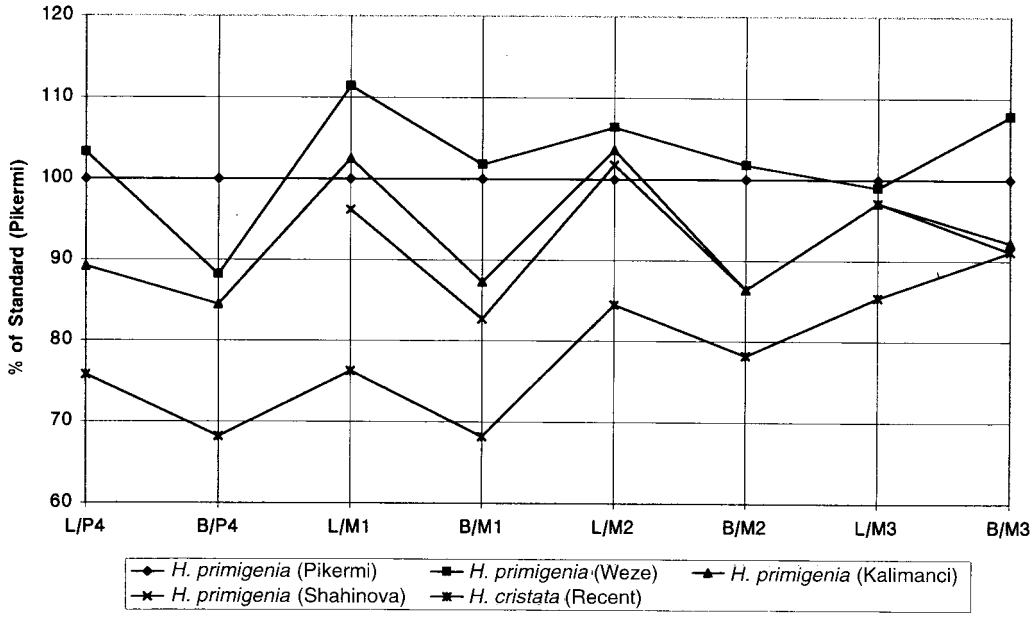

Figure 4. Scatter diagram of Hystricids lower postincisive teeth relative dimensions, with *Hystrix primigenia* from Pikermi taken as 100%. (Data and references in Table 2).

(I.S.), calculated as Width x 100/ Length of the tooth. Comparison of these indices for *H. primigenia* from Pikermi, Kalimanci and Shahinova reveal that I.R. tends to decrease from M_1 to M_3 (Fig. 5). The same index calculated for the recent species *Hystrix cristata* shows the reverse trend; it increases in size towards the last molar (Fig. 6). Since the known sample sizes are modest, it is not safe to draw a definite conclusions from these trends. The same comparison performed for the upper teeth, shows that the samples from Pikermi, Dytico-3 and Kalimanci are displaying similar index, while the specimens from Weze, Poland display quite different I.R. (data in Table 2).

The comparison of the lower teeth occlusal morphology is presented in figure 7. The thickness of the enamel ridges in the *Hystrix primigenia* teeth from Shahinova, Albania varies from 0.9 mm to 10.0 mm, while the enamel ridges of *Hystrix* cf. *vinogradovi* teeth measure only 0.3 - 0.4 mm. In all Neogene samples a large enamel ridge is observed, which seems to be characteristic for these large bodied animals (Fig. 7).

The Albanian specimen displays a yellow enamel on the incisor. This feature is also observed in Villafranchian specimens of *Hystrix major*, the incisors of which retained a "coloration jaune pale" (GERVAIS 1859). It is probable that this pigmentation is connected more with diet than with anything else.

Based on biochronological and stratigraphical data, we assign the lowermost levels of the Shahinova quary a Late Miocene – Early Pliocene age. In addition, there are depositional similarities with the site of Pikermi. Both sites are located not far from the sea, they present calcareous deposits affected by karst fissures, and both preserve rich mammal fossil samples.

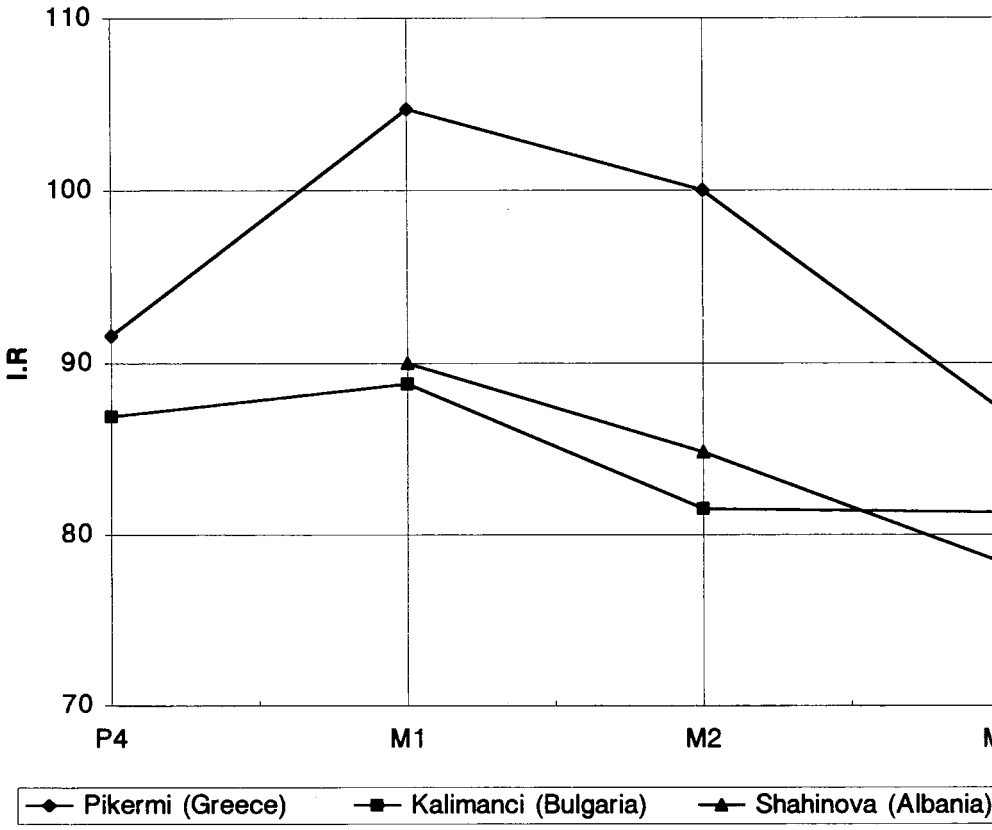

Figure 5. Scatter diagram of Index of Robusticity (I.R. =W/L x100) of *Hystrix primigenia* lower postincisive teeth from Pikermi, Kalimanci and Shahinova. (Data and references in Table 2).

Paleoecology

Porcupines are simplicidentales, i.e., they present one pair of upper and one pair of lower incisors. They show a wide range of adaptations, as well as geographical and chronological distribution among the gnawing rodents (WILSON & al. 1984). It is widely accepted that *Hystrix* appeared first in the Oligocene of Europe (ROMER 1974; NOWELS 1991). Many porcupine species have been described from Late Miocene to Pleistocene. A distinct decrease in tooth size is observed between the Late Miocene – Early Pliocene *Hystrix primigenia* and the Pleistocene crested-tooth *Hystrix cristata*. Villafranchian forms of *Hystrix* seem to be closer in size to *Hystrix primigenia* rather than to Pleistocene forms.

Studies on recent discoveries such as this presented here, underline the biochronological importance of *Hystrix primigenia* as a characteristic Late Miocene species in eastern Europe, since they offer evidence that *Hystrix* occurred earlier in North Africa and eastern Europe than it did in western Europe (MN 15, MEIN 1989). Also the taxon has a strong biogeographical presence in South Europe, such as in Greece and adjacent areas

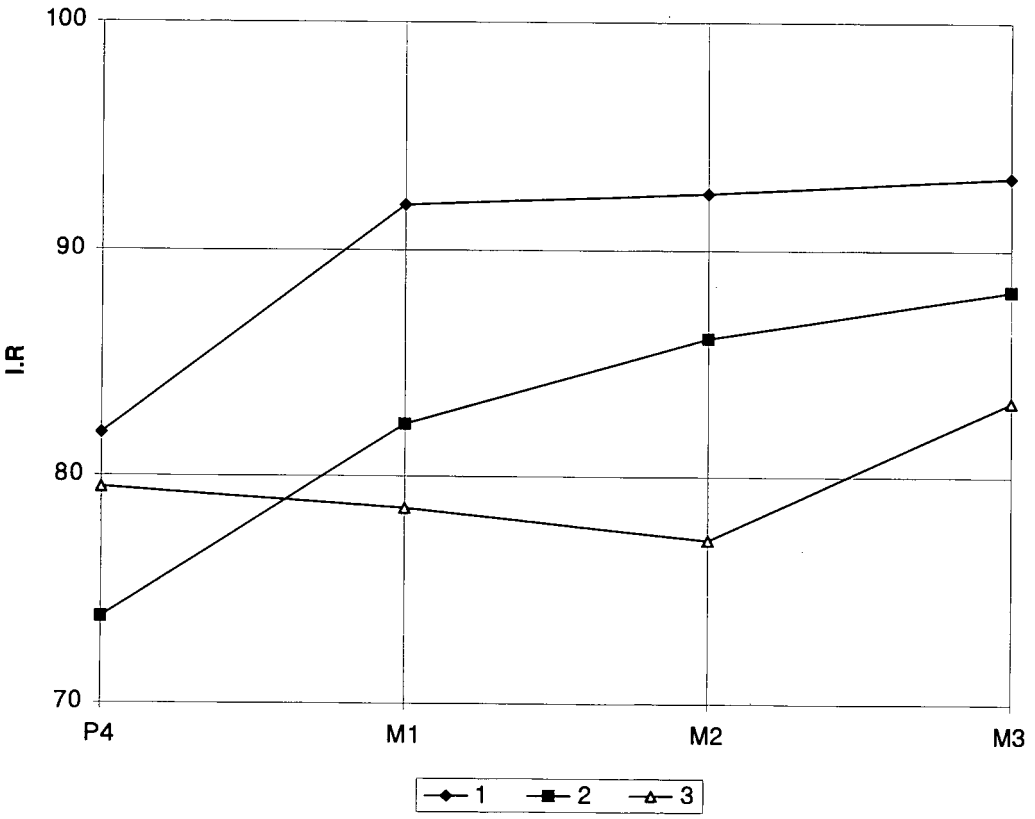

Figure 6. Scatter diagram of Index of Robusticity (I.R. =W/L x100) of recent *Hystrix cristata* lower postincisive teeth from Europe (1), from north Africa (2), and *H. cristata* including *H.* cf. *indica* (3). (Data and references in Table 2).

of the Balkan peninsula. Except from Pikermi, the type locality (including the Chomateri locality - BACHMAYER & al. 1982), fossils have been recorded and described from the Greek localities of Samos (SOLOUNIAS 1981), Halmyropotamos in Evia (MELENTIS 1967), Alifakas in Thessaly (MELENTIS & al. 1966), and in Dytiko 3 – in Axios Valley – in Macedonia (BONIS de & al. 1988; KOLIADMIOU & al. 1991); from Shahinova, Albania; from Kalimanci, Bulgaria (NIKOLOV 1983); and from Umen Dol in ex-Yugoslavia; from Kemiklitepe, Turkey; from Weze, Poland; Monticino, Italy; from Layna and Villarroya, Spain (references cited above). It is reasonable to suppose that during the latest Miocene, at the time of the Mediterranean salinity crisis, one of the cross-roads connecting Africa and Asia was the greater area of the Balkan peninsula.

Remains of *Hystrix* s.l., are known throughout the rest of Europe at the time of Plio-Pleistocene boundary (Villafranchian). For example from Tegelen, Villany, Etouaires, Saint-Vallier (VIRET 1954), Val d'Arno, Olivola and Erpfingen. (de BRUIJN & al. 1992). Outside Europe, Hystricidae fossils are reported from North sand West Africa. (SAVAGE & al. 1983). Some of these species agree in size with *Hystrix primigenia* from Pikermi (measurements in GREENWOOD 1955).

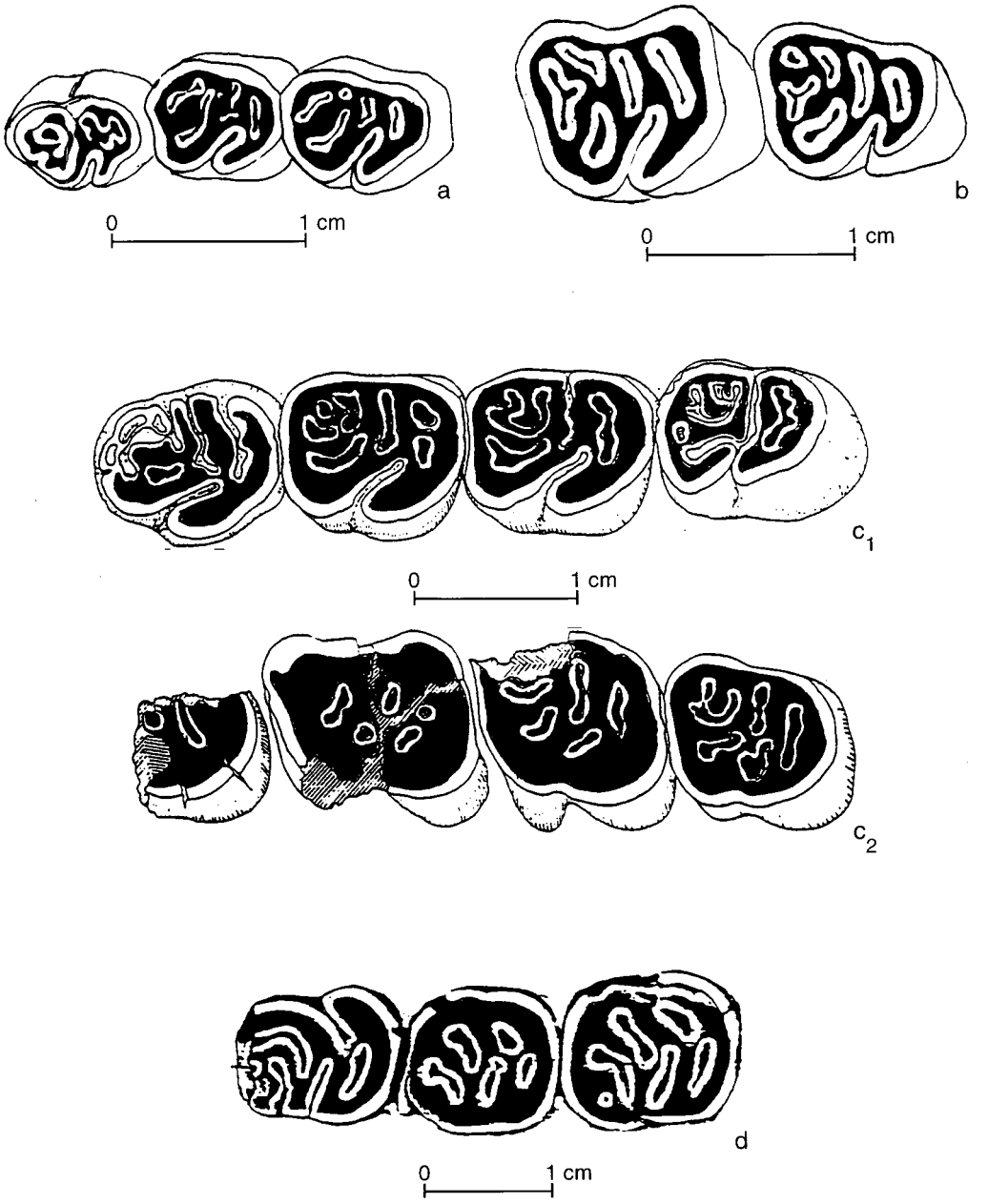

Figure 7. Comparison of *Hystrix primigenia* lower teethraw occlusal morphology and dimensions (in mm) from different European sites. A: LP_4, LM_1, LM_2, LPH 82/6, *H.* cf. *vinogradovi* from Gajtan 1, (north Albania, Middle Pleistocene). B: LM_2, LM_3, LPH 85/7, *H. primigenia* from Shahinova (south Albania, Late Miocene - Early Pliocene). $C_{1\text{-}2}$: LP_4-LM_3 of two old individuals of *H. primigenia* from Kalimanci level IV, Bulgaria (from SEN & al. 1987, fig. 3). D: RP_4-RM_2 of *H. primigenia* from Weze, Poland (from SULIMSKI 1960: Pl.II, fig.5).

Based on morphological features, we observe similarities as well as differences in life style and in geographical distribution between fossil and extant porcupines of the Old World. Pleistocene porcupines are found in Europe mostly as part of interglacial faunal assemblages (JANOSSY 1963-64). The crested porcupine inhabits mostly dry open areas and in particular hill slopes. The Mio-Pliocene *Hystrix primigenia* seems to have been adapted to warm dry climate inhabiting rugged lowland terrain. This was the environment in which *H. primigenia* lived in Albania during this time period.

The decrease of the Index of Robusticity posteriorly in *Hystrix primigenia* chick teeth during the Miocene and Pliocene Epochs, reveal possible differences in feeding behaviour from *Hystrix cristata*, in which the I.R. raises towards the last molars. It is possible that during the time period from Late Miocene to Early Pliocene, a southward animal migratory wave took place in Eurasia towards Africa, in search for warmer and more favourable environments.

In describing the Pikermi site, GAUDRY (1856) underlines that Greece is connected to Europe through a series of mountains, of which Albania is also part. Pikermi and Shahinova, therefore, are geologically related in addition to being geographically close (ca 500 Km distance). Furthermore, similar degree of faunal composition to that of Pikermi is encountered in the Shahinova quarry faunal sample (under study by FISTANI). These similarities between the Shahinova and Pikermi sites can support the hypothesis that the accumulation of Shahinova faunal assemblage is a result of taphonomic events similar to the catastrophic which occurred in Pikermi during the Late Miocene.

Recent porcupines are herbivorous and frequently are considered 'solitary' because they are nocturnal. The gnawing behaviour of porcupines is not a simple vicissitude. It is considered rather, an important taphonomic agent and paleoecological indicator. By collecting bones from different cadavers they maintained their incisors sharp. *H. primigenia*'s need for bones can be satisfied only in a paleoecologically and faunally rich environment. This animal must have lived, therefore, in a rich habitat such as the African savannah, which, in fact, *H. cristata* inhabits today. Finally, it was terrestrial and walked on the sole of its foot.

In South - West Albania *H. primigenia* lived in a mountainous area rich in forests and open woodland – bushland environments, in the Periadriatic Depression not far from the Adriatic sea. The recovery of the Middle Pleistocene *Hystrix* cf. *vinogradovi* in the site Gajtan 1 in North Albania (FISTANI 1994) shows that this species inhabited rock shelters. The same habitat is preferred by *H.* cf. *indica*, found in the rock shelter of Ksar Akil in Lebanon (HOOIJER 1961). The Shahinova site is part of a karst, hence many fissures and caves are present there. These data support the idea that this presumably nocturnal rodent, *H. primigenia*, was also sheltered in natural or self-made (excavated) dens in caves and crevices. Although fat, these ponderous animals were sensitive to cold. Large bodied porcupines such as *H. primigenia*, might have become inactive during the cold months of winter. The search for warm habitats with rich faunas must be considered as the major paleoecological factors of *Hystrix primigenia*.

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