

THE HYSTRICIDAE FROM THE PLEISTOCENE OF MACEDONIA (GREECE) AND A REVIEW OF THE EUROPEAN REPRESENTATIVES OF THE FAMILY

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A B S T R A C T

Some specimens of Hystricidae from the Pleistocene of the Mygdonia basin (Macedonia, Greece) are studied. Their morphological features allow us to identify these as *Hystrix major* GERVAIS, 1859. The taxonomy of the European representatives of the genus *Hystrix* are discussed and the relevance of the various species for the biostratigraphy of the Neogene is reviewed.

Σ Υ Ν Ο Ψ Η

Στην εργασία αυτή μελετώνται μερικά δόντια της άνω γνάθου και μία κάτω γνάθος Hystricidae από το Πλειστόκαινο της λεκάνης της Μυγδονίας (Μακεδονία). Τα μορφολογικά χαρακτηριστικά των δοντιών καθώς και η σύγκριση τους με το γνωστό υλικό του Νεογενούς-Τεταρτογενούς της Ευρώπης δείχνουν, ότι ανήκουν στο είδος *Hystrix major* GERVAIS, 1859. Επίσης γίνεται μια προσπάθεια συστηματικής ταξινόμησης των γνωστών μέχρι τώρα δειγμάτων από την Ευρώπη και στο τέλος επιχειρείται η ανασκόπηση της στρωματογραφικής εξάπλωσης του γένους στο Νεογενές.

INTRODUCTION

One of the few well known Pleistocene localities of central Macedonia (Greece) is the locality "Gerakarou-1", GER (ZAMANIS et al., 1980; KOUFOS & MELENTIS, 1983). The locality is situated in the Mygdonia basin and near the village of Gerakarou, 35 km east of Thessaloniki (fig. 1).

ΚΑΛΛΙΟΠΗ ΚΟΛΙΑΔΗΜΟΥ & ΓΕΩΡΓΙΟΣ Δ. ΚΟΥΦΟΣ. Τα Hystricidae από το Πλειστόκαινο της Μακεδονίας (Ελλάδα) και μια ανασκόπηση των αντιπροσώπων της οικογένειας στην Ευρώπη.

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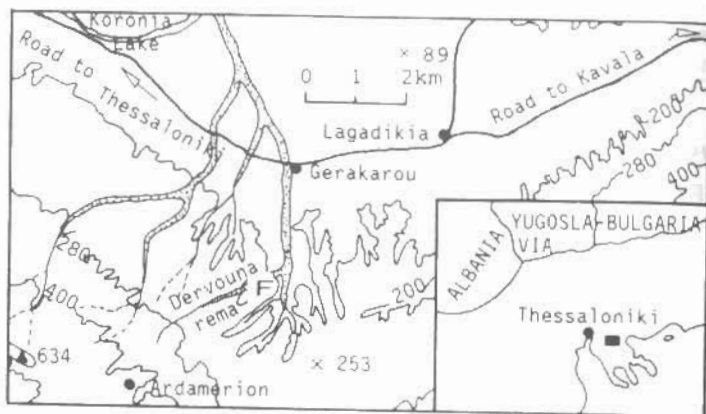


Fig. 1. Sketch map indicating the position of the locality Gerakarou-1 (GER) in the Mygdonia basin.

Σχ. 1. Χάρτης της Μυγδονίας λεκάνης, με τη θέση εύρεσης των απολιθωμάτων

The basin was filled during Neogene-Quaternary by sediments which were divided into two groups (PSILOVIKOS, 1977).

-The **Premygdonian Group**, consisting of conglomerates, sandstones, sands, silts, and red-beds. These sediments are of late Miocene-early Pleistocene age.

ZAMANIS et al. (1978)	KOUFOS & MELENTIS (1983) KOUFOS (1986a, 1986b, 1988 in prep.)
Cervide de la taille de <i>Cervus philisi</i> .	<i>Pliohyaena brevirostris</i> .
Bovide de la taille de <i>Procampoceras brivatense</i> .	<i>Pliohyaena perrieri</i> .
<i>Gazella</i> sp.	<i>Meles</i> sp.
<i>Gazellospira</i> sp.	<i>Canis etruscus</i> .
<i>Equus</i> cf. <i>stenonis</i> .	<i>Canis arnensis</i> .
<i>Mimomys</i> sp.	<i>Equus stenonis</i> .
Hyaenide ind.	<i>Sus strozzii</i> .
	<i>Croizetoceros ramosus</i> cf. <i>minor</i> .
	<i>Eucladoceros senezensis senezensis</i> .
	<i>Cervus</i> cf. <i>philisi</i> .
	<i>Gazella borbonica</i> .
	<i>Gazellospira</i> sp.

Tab. 1. List of the Gerakarou-1 fauna.
Πιν. 1. Κατάλογος απολιθωμάτων που βρέθηκαν στην απολιθωματοφόρα θάλασσα Γερακάρου-1

-The **Mygdonian Group**, consisting of gravels, sands, silts and alluvial deposits. These sediments are of middle Pleistocene-Holocene age.

The red-beds of the Premygdonian Group were named Gerakarou Formation (KOUFOS et al., 1989). The transition from Premygdonian to Mygdonian Group sometimes is sudden with a conglomerate at the base and sometimes gradual. The red-beds of the upper part of the Premygdonian group are loose reddish sands which are alternating with grey marls and massive, tuffaceous, white limestones. The transitional zone between the two groups has been named Platanochori Formation (KOUFOS et al., 1989). The fossiliferous beds of the Gerakarou locality, situated in the upper part of the Gerakarou Formation, are concentrations of bones of various species mixed together. In some cases articulated bones were found e.g. metapodials with the first phalanx or metapodials with some tarsals or carpals.

The first collection from Gerakarou was poor. Later excavations in GER yielded a rich material, which allows more accurate descriptions and identifications (Tab. 1).

TAXONOMY

Order : Rodentia BOWDICH, 1821.
Superfamily : Hystricoidea GILL, 1872.
Family : Hystricidae BURNETT, 1830.
Genus : *Hystrix* LINNE, 1758.

Hystrix major GERVAIS, 1859.

Synonyms : 1859 *Hystrix major* GERVAIS.
1898 *Hystrix etrusca* BOSCO.
1910 *Hystrix major* HARLE.
1972 *Hystrix* cf. *major* CHALINE.
1987 *Hystrix major* AGUSTI et al.

Locality : "Gerakarou-1", (GER), Macedonia, Greece.
Age : Late Villafranchian (Biharian).
Material : Left mandibular fragment with I-M/2, GER-170; right upper incisor, GER-171; right P4/, GER-172; left P4/, GER-173; left M3/, GER-174; right M3/, GER-175.

Diagnosis: Slightly smaller than *H. primigenia*; complicated synclinid I; rounded occlusal surface of the cheek teeth; slender cheek teeth.

DESCRIPTION

1. Upper cheek teeth.
The studied upper cheek teeth possibly belong to the same individual because the dimensions and stage of wear are similar. I2/ : Strongly curved with triangular transverse section. The enamel covers the anterior surface of the tooth and it is

continued as far as the middle of the buccal surface. This enamel development is characteristic for all Hystricidae. The shape and dimensions of the specimen are given in fig. 2.

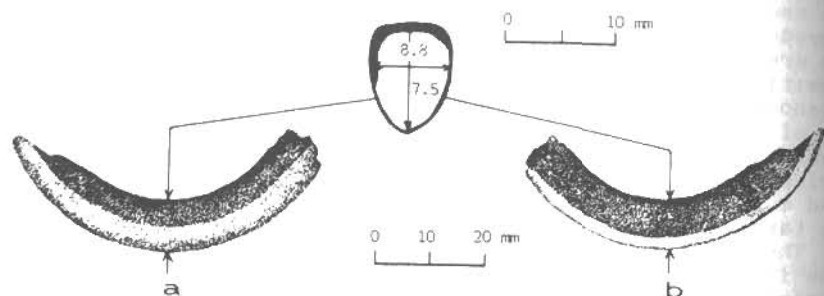


Fig. 2. *Hystrix major*, Gerakarou-1 (GER), right upper incisor, GER-171; a. buccal and b. lingual view.

Σχ. 2. *Hystrix major*, Γερακαρού-1 (GER), δεξιός άνω κοπήρας, GER-171, α. εξωτερική και β. εσωτερική όψη.

For the description of the cheek teeth the nomenclature given by AGUSTI et al. (1987, p.100, fig. 3) is used.

P4/: High-crowned and curved buccally with suboval occlusal surface. The tooth is divided into two lobes, the anterior and the posterior one, by two sinuses. The lingual sinus is stronger than the labial one and extends from the occlusal surface to the root. The buccal sinus is less developed and disappears at about 11.5 mm from the root. The anterior lobe has a rounded anterior border. The narrow mesio-buccal sinus extends as far as the root. The syncline I, situated in the anterior lobe, is divided into two islets, an elongated buccal one and a rounded one in the center of the lobe. In GER-173 the syncline I is clearly connected with the narrow mesio-buccal sinus of the anterior lobe (fig. 3). As wear progresses the syncline I is becoming an enamel islet. The syncline II corresponds to the main lingual sinus. It is still open in GER-173, while it is in touch with the enamel border in GER-172 (fig. 3). It is elongated and narrow reaching the middle of the tooth's breadth. The syncline III consists of two unequal islets. The longer one is situated lingually. Its longitudinal axis is more or less parallel to the lingual enamel border of the posterior lobe and to the sinus. The other islet is crescent shaped and about parallel to the syncline II. The syncline IV is oval-shaped and it is situated in the distobuccal corner of the tooth.

M3/: High-crowned and curved buccally with triangular occlusal surface. The division of the tooth in two lobes is not so



Fig. 3. *Hystrix major*, Gerakarou-1 (GER), a. right P4/, GER-172; b. left P4/, GER-173; occlusal view.

Σχ. 3. *Hystrix major*, Γερακαρού-1 (GER), α. δεξιός P4/, GER-172, β. αριστερός P4/, GER-173, μαστική όψη.

clear. The buccal sinus has completely disappeared, while the lingual one is well developed (fig. 4). The anterior lobe is very small. The posterior one is larger with rounded distal border. The syncline I, situated in the anterior lobe, is crescent shaped in GER-175. In GER-174, which is more worn, the syncline I is

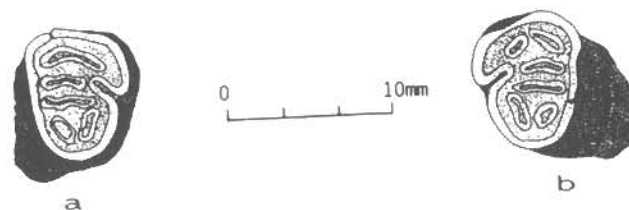


Fig. 4. *Hystrix major*, Gerakarou-1 (GER), a. right M3/, GER-175; b. left M3/, GER-174; occlusal view.

Σχ. 4. *Hystrix major*, Γερακαρού-1 (GER), α. δεξιός M3/, GER-175, β. αριστερός M3, GER-174, μαστική όψη.

divided in two elliptical islets. The syncline II is elongated, narrow and parallel to the syncline I, situated between the buccal enamel border and the lingual sinus. The syncline III is divided into two islets, whose longitudinal axes form an acute angle. The larger one of these two islets is parallel to and longer than syncline II. In GER-175 it is in touch with the buccal enamel border. The smaller islet is situated in the posterior lobe. Its longer axis is parallel to the lingual enamel border of the tooth. The syncline IV is a rounded small enamel islet, situated in the disto-lingual part of the tooth.

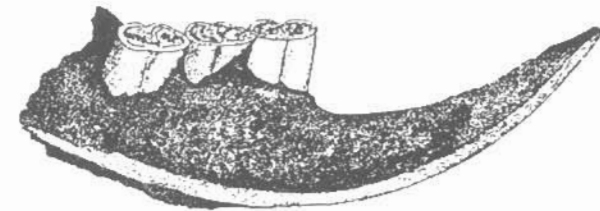
2. Mandible.

The mandible belongs to an adult individual. The ramus is high under the cheek teeth but becomes gradually shallower in front of the premolar. The height of the ramus below the cheek teeth fluctuates from 26 to 27 mm. The single mental foramen is situated in front of P/4. The masseteric fossa is quite strong and its anterior border is situated below the labial sinus of M/1.

The incisor is directed anteriorly and buccally. The incisor traverses all the inferior part of the mandibular ramus and ends below the M/3. The occlusal length of the tooth row P/4 - M/2, is 33,2 mm. The occlusal surface of the tooth row declines from P/4 to M/2 because of attrition. The longitudinal axis of the tooth row forms an angle of about 15° with the incisor.

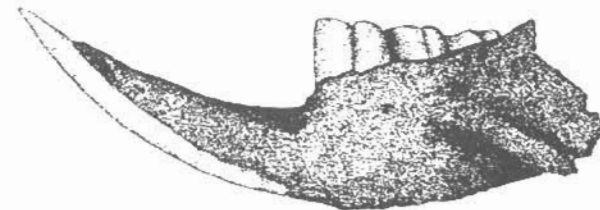
P/4 : The occlusal surface is parallelogram shaped with rounded corners. The main sinus is deep and extends from the occlusal surface to the root across the buccal border of the tooth. Another sinus with the same characters, but less deep is situated lingually. This is the equivalent of the synclinid III (fig. 5). These two sinuses divide the tooth into two lobes, the anterior and the posterior one. The anterior lobe, longer and narrower, than the posterior one, contains the synclinids I and II. Its anterior border is rounded with a very shallow mesio-buccal sinus. The synclinid I is quite complicated and becomes divided into two or three islets as the attrition progresses. The synclinid II consists of three, more or less oval islets which are in touch with each other. The longer axis is crescent shaped. The synclinid III is separated from the lingual sinus. It is a simple, elongated enamel islet, reaching to the middle of the tooth's breadth. Its longer axis is at right-angles to the tooth's length. The synclinid IV, an elongated and quite complicated enamel islet, is parallel to the distal border of the tooth. It is the only synclinid that situated in the posterior lobe.

M/1 : The occlusal surface is rectangular and slightly wider than that of the P/4. Its corners are rounded, specially buccally. On the occlusal surface the buccal sinus is closed and forms an oval enamel islet which is situated in the posterior lobe (fig. 5). The buccal and lingual sinuses are well defined in the corresponding walls of the tooth. The synclinid I is very complicated. It consists of a pair of small, rounded enamel islets, situated in the mesio-lingual corner of the tooth and of an

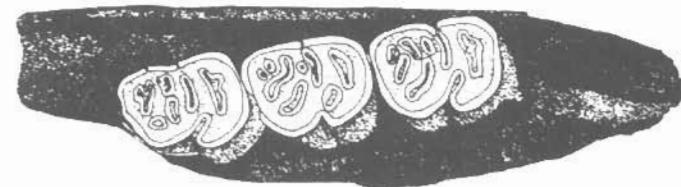


a

0 10 20mm



b



c

0 10mm

Fig. 5. *Hystrix major*, Gerakarou-1 (GER), mandible. GER-170; a. lingual, b. buccal and c. occlusal view.

Σχ. 5. *Hystrix major*, Γερακαρού-1 (GER), κάτω γνάθος. GER-170. α. εσωτερική, β. εξωτερική και γ. μασητική όψη.

	Hystrix		Hystrix		Hystrix		Hystrix		Hystrix		Hystrix	
	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
P ₄	11.20	12.22	13.00	10.65	9.30	11.00	11.00	10.50*	11.50	10.70	12.30	10.00
M ₁	8.75	9.88	9.64	7.90	7.20	9.00	9.00	7.30*	9.40	9.30	10.60	10.00
M ₂	8.80	10.42	10.84	-	10.90	10.00	-	-	12.30	9.80	10.30	10.00
M ₃	11.15	10.88	10.62	-	9.80	11.00	9.50	-	9.20	9.10	10.00	10.00
R.I., P ₄	78.1	80.9	74.2	74.3	77.4	11.8	81.8	-	81.7	-	86.1	-
R.I., M ₁	79.3	81.2	78.4	-	83.5	90.0	-	-	89.3	82.9	87.3	87.1
R.I., M ₂	81.6	84.8	87.0	-	86.7	81.8	73.7	-	86.4	80.2	81.6	89.5
R.I., M ₃	-	84.0	-	-	-	88.9	71.7	-	88.9	84.9	81.4	81.5

*Measurements from photos.
Μετρήσεις από φωτογραφίες.

Tab.2. Dimensions of the lower cheek teeth of fossil Hystrix.
Πιν.2. Διαστάσεις των δοντιών της κάτω γνάθου των απολιθωμένων αντιπροσώπων του Hystrix.

	Hystrix		Hystrix		Hystrix		Hystrix		Hystrix		Hystrix		Hystrix	
	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
P ₄	11.45	11.65	-	8.86	9.86	11.00	8.70*	22.40	12.70	11.80	11.70	11.45	11.00	11.00
M ₁	9.75	9.70	-	7.32	8.35	10.00	7.85*	12.20	12.80	12.10	12.40	-	-	-
M ₂	-	-	-	12.26	-	9.00	-	8.85	-	-	-	-	-	-
M ₃	-	-	-	8.34	-	10.00	-	12.15	-	10.00	10.00	-	-	-
R.I., P ₄	85.2	84.7	-	9.40	9.60	10.50	8.00*	12.30	12.45	9.86	10.50	9.50	9.70	94.4
R.I., M ₁	-	-	-	82.6	84.6	90.9	90.2*	94.6	108.7	-	120.5	111.9	-	-
R.I., M ₂	-	-	-	81.3	-	111.1	76.0	137.3	-	-	-	-	-	-
R.I., M ₃	-	-	-	-	-	105.0	79.5	123.0	125.8	93.6	126.0	-	-	-
R.I., M ₃	-	-	-	86.2	83.3	80.0	62.5*	-	-	-	127.3	-	-	102.1

*Measurements from photos.
Μετρήσεις από φωτογραφίες.

Tab. 3. Dimensions of the upper cheek teeth of fossil Hystrix.
Πιν. 3. Διαστάσεις των δοντιών της άνω γνάθου των απολιθωμένων αντιπροσώπων του Hystrix.

S-shaped one, (fig. 5). These three islets are situated very close to each other. The synclinid II consists of two islets. One very small and rounded, situated between the synclinid III and the S-shaped islet of the synclinid I, the other elongated with its longitudinal axis parallel to the buccal sinus. The synclinid III is also elongated and narrow. It is situated near to the lingual enamel border and it is in touch with it. The synclinid IV is less complicated than in the other lower cheek teeth. Its longitudinal axis, is in part parallel to the distal enamel border and in part parallel with the lingual enamel border (fig. 5.). Thus it has a triangular shape.

M/2 : The occlusal surface is rectangular with rounded corners. Its pattern is clearly divided into two lobes. The anterior lobe is bigger and more robust than the posterior one, being 3/4 of the tooth's length. The buccal sinus is deep and directed backwards, while the lingual one, corresponding to the synclinid III, is more or less transverse (fig. 5). The synclinid I is complicated and divided in three sub-oval enamel islets, situated in the mesio-lingual corner of the occlusal surface. Two of the islets are of equal size, while the third one is smaller. The synclinid II consists of two islets, exactly as in the M/1. The smaller islet is situated between synclinid I and III and the biggest one, crescent shaped, is parallel to the buccal sinus. The synclinid III, corresponds to the lingual sinus. The synclinid IV is elongated and quite wide.

DISCUSSION

A number of hystrioids were described from Neogene-Quaternary of Europe under various specific names. A lower incisor from Pikermi was first described under the name *Lamprodon primigenius* (WAGNER, 1848); later two isolated cheek teeth were described under the name *Castor atticus* (ROTH & WAGNER, 1854) and farther a mandible with the morphological features of both above mentioned specimens was described under the name *Hystrix primigenia* (GAUDRY & LARTET, 1859). Later on WAGNER (1857) accepted the last name. GAUDRY's paper (1862-67, p. 122, pl. XVIII, fig. 1-4), does not fully describe the tooth collection however the following observations can be made from his illustrations and how they differ from material studied in this paper:

- the GER material shows a more rounded tendency in the corners of the occlusal surface of the cheek teeth
- the synclinid I of GER material has a more complicated enamel pattern.

- the studied cheek teeth exhibit an elongated aspect ratio of the occlusal surface in respect to GAUDRY's material while maintaining the same tooth height (tab. 2, fig. 6)

A mandible from the Turolian locality of Halmyropotamos (southern Greece) was described as *H. primigenia* by MELENTIS (1967). These teeth show the same differences from the Gerakarou, as those for the Pikermi material, referred above.

Recently some mandibular fragments and isolated cheek teeth from the late Miocene of Kalimanci locality in Bulgaria have

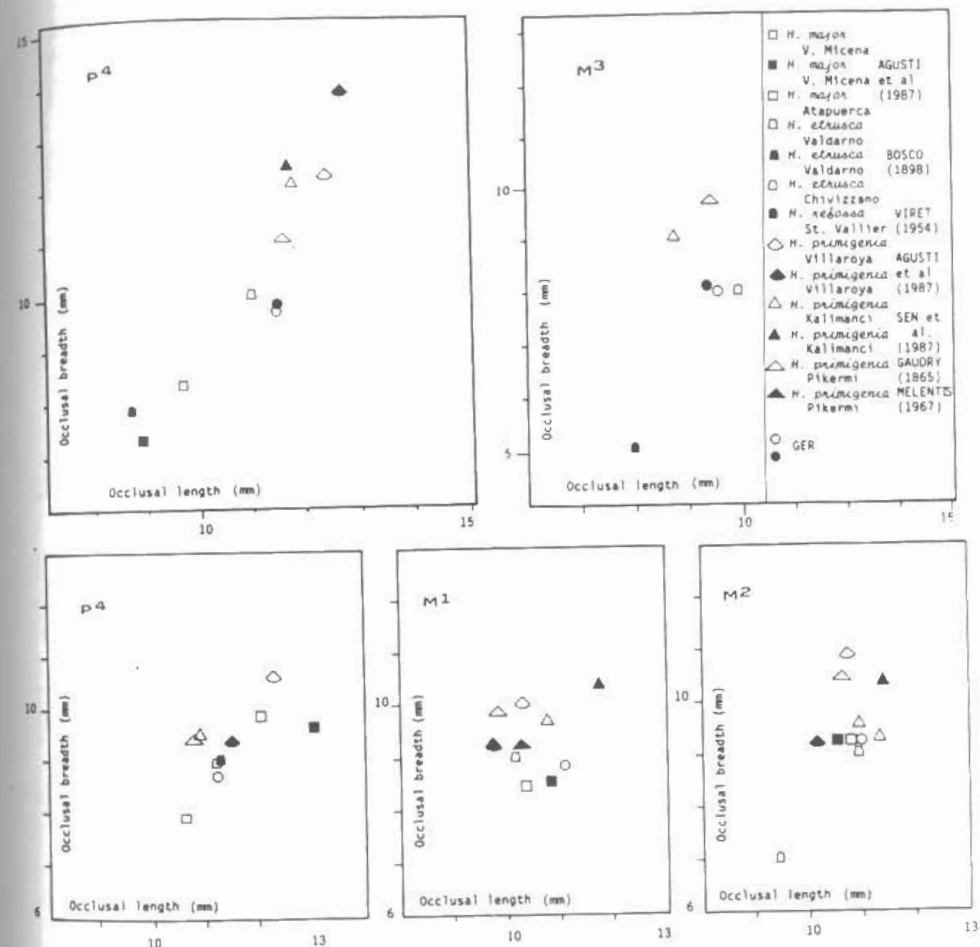


Fig. 6. Scatter diagram occlusal length/occlusal breadth for the upper and lower cheek teeth of *Hystrix* from various localities.

Σχ. 6. Συγκριτικό διάγραμμα μήκους/πλάτους της μαστικής επιφάνειας των δοντιών της άνω και κάτω γνάθου του *Hystrix* από διάφορες απολιθωματοφόρες θέσεις.

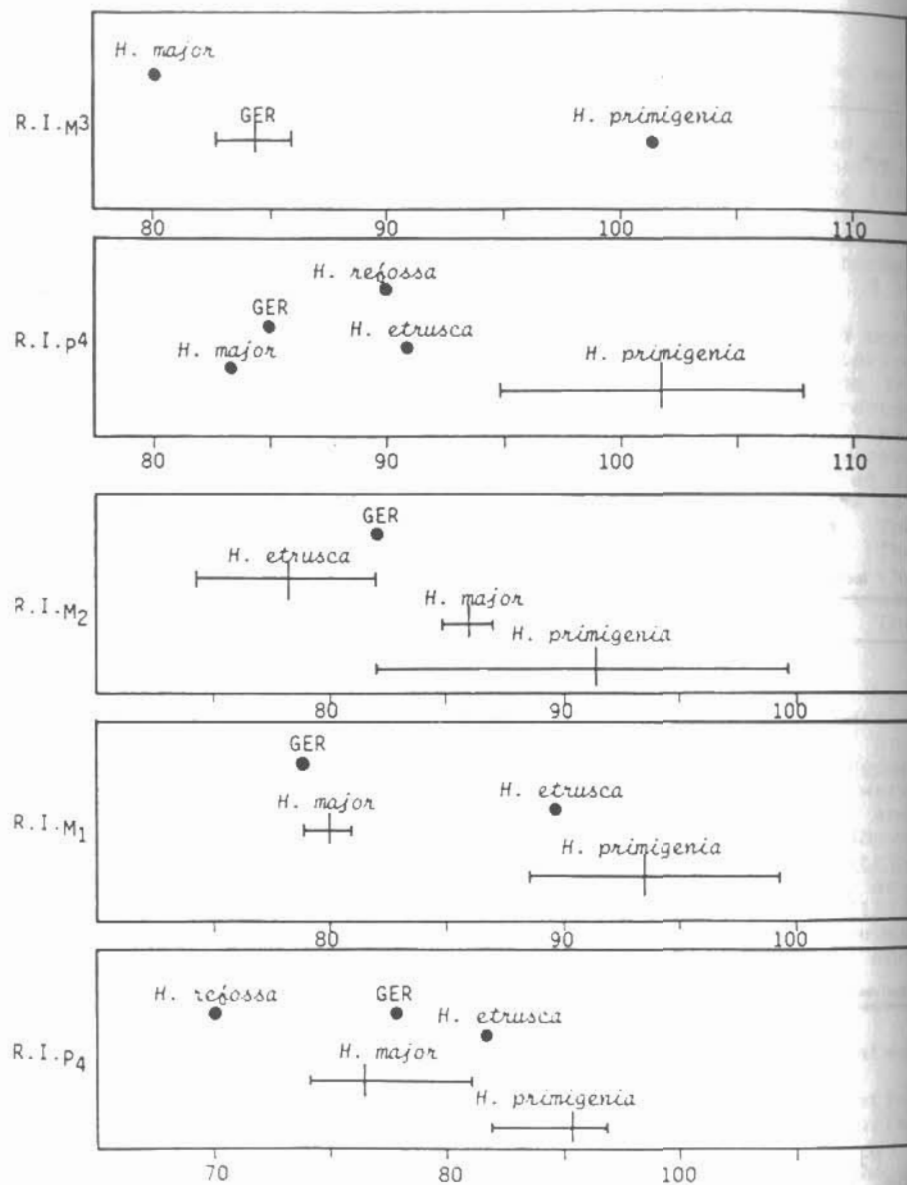


Fig. 7. Robusticity index for the cheek teeth of various species of *Hystrix*

Σχ. 7. Δείκτης ευρωστίας για τα μαστικά δόντια διαφόρων ειδών του *Hystrix*.

been described as *H. primigenia* (SEN et al., 1987). These specimens represent a larger stage of wear than our material except one mandibular fragment (SEN et al., 1987, fig. 3a). Thus it is not easy to compare the morphology and dimensions of the samples. Nevertheless the higher robusticity index of the Bulgarian material distinguishes it from the Gerakarou one (tab. 2, fig. 6).

DEPERET (1890) described some mandibular fragments and isolated teeth from the Pliocene locality of Roussillon under the name *H. primigenia*. This material shows the same differences from the Gerakarou one as those of Pikermi material.

Some material of *H. primigenia* is also known from the late Pliocene localities of Layna and Villaroya (AGUSTI et al., 1987). The less rounded tendency in the corners of the occlusal surface of these teeth as well as their high robusticity indices distinguish these clearly from the GER material (tab. 2).

A mandibular piece with P/4 from the locality of Perrier was described under the name *H. refossa* (GERVAIS, 1848-52, pl. XLIII, fig. 11). The differences between this P/4 and GER material are not significant. Later a maxilla and an isolated upper incisor from St. Vallier were described as *H. refossa* (VIRET, 1954, pl. 16, fig. 4-6). No differences between the incisors from St. Vallier and GER could be observed. The P4/ from St. Vallier is morphologically very similar to our material. The M3/ from St. Vallier is unworn and a comparison of the enamel pattern with the specimens from GER is difficult. The St. Vallier teeth exhibit also a more elongated aspect ratio of the crown area in respect to *H. primigenia*.

After some years GERVAIS (1859) described from the Quaternary deposits of Ratoneau (France) an isolated upper incisor, which was larger than that of Perrier. He supposed that it represents a larger species than *H. refossa* and he erected the new species *H. major*. Later another upper incisor from the Quaternary of Montejeau (France) was identified as *H. major* (HARLE, 1910). Both incisors are similar to that from Gerakarou especially that from Montejeau.

Recently abundant material, from the early Pleistocene of Venta Micena (Spain), was described as *H. major* (AGUSTI et al., 1987). The detailed description of the Venta Micena material allows a comparison with our material. The GER teeth have similar morphological features of the enamel pattern with the Venta Micena material; especially the complicated pattern of the synclinid 1 is similar in both samples. The robusticity indices of the cheek teeth for both samples are similar and smaller than those for *H. primigenia* (tab. 2, fig. 6). These morphological and metrical similarities of the Gerakarou and Venta Micena material show that they represent the same species.

BOSCO (1898) described the species *H. etrusca* from the Villafranchian of Valdarno (Italy). The Valdarno material differs from *H. primigenia* in having more slender teeth and a smaller M/3 (fig. 6). These do not seem to be significant differences between *H. etrusca* and *H. major*. *H. refossa* seems to have dif-

ABSOLUTE AGE M.a.	S E R I E S	CONTINENTAL STAGES	MN ZONES	LOCALITIES	H Y S T R I X
1.8	P L E I S T O C E N E	BIHARIAN	17	GERAKAROU-1 Venta Micena Upper Valdarno	Hystrix major
		VILLAFRANCHIAN VILLANYIAN	16	St. Vallier Villaroya Etouaires	
	R U S C I N I A N	15	Layna Perpignan	Hystrix primigenia	
5.5	U P P E R M I O C E N E	R U S C I N I A N	14		Hystrix primigenia
		T U R O L I A N	13	Samos Q ₅ ? Dytiko - 3	
		T U R O L I A N	12	Taraklia Pikermi Kalimanci Halmyropotamos ? Alifakas ?	
		T U R O L I A N	11	Samos Q ₁₋₄ ?	

Tab. 5. Stratigraphic distribution of *Hystrix* in Neogene-Quaternary of Europe.

Πιν. 5. Στρωματογραφική εξάπλωση του γένους *Hystrix* στο Neογενές-Τεταρτογενές της Ευρώπης.

ferent crown morphology than *H. etrusca* but this may be due to the different stage of wear. This was possibly the reason for BOSCO to consider the Valdarno material as a new species. Thus *H. etrusca* is synonymized with *H. major*.

CHALINE (1972) described some hystricid specimens from Vallonet (France) as *H. cf. major* because he considered these to be larger than *H. refossa* from St. Vallier. The Vallonet material has a crown morphology and robusticity indices very similar to the GER specimens and thus we consider this belonging to *H. major*.

The comparison of the GER material indicates that the studied *Hystrix* is different from *H. primigenia* and closer to *H. major*.

TAXONOMY AND BIOSTRATIGRAPHY OF *HYSTRIX*

The comparisons of the known Neogene-Quaternary material of *Hystrix* from Europe indicate the presence of two species: *H. primigenia* and *H. major*; the main characters of these are given in Tab. 4. The presence of a third species, *H. refossa*, is also referred but the few known specimens (an isolated P4/ from Perrier and a left maxilla with P4/-M3/ from St. Vallier) and the absence of a good sample of upper cheek teeth from GER, cannot allow us to consider this as a separated species or as a synonym to *H. major*. Nevertheless a more rich collection from the Neogene and Quaternary of Europe will allow us to have a better knowledge about the species number, the morphology and the variation of the dimensions of *Hystrix*.

CHARACTERS	<i>Hystrix primigenia</i> (WAGNER, 1848)	<i>Hystrix major</i> (GERVAIS, 1859)
Size	Large	Medium
Occlusal surface	More or less quadrangular shaped with acute corners	With rounded corners
Synclinalid I	Simple	Complicated
Robusticity of the teeth	Robust	Slender

Tab. 4. Morphological characters distinguishing *H. primigenia* from *H. major*.

Πιν. 4. Διακρίση των *H. primigenia* και *H. major* με βάση ορισμένα μορφολογικά χαρακτηριστικά τους.

The stratigraphically oldest species is *H. primigenia* and the type material comes from Pikermi. The same species is also known from Samos (SOLOUNIAS, 1981) as well as from Halmyropotamos

(MELENTIS, 1967) and Alifakas (MELENTIS and SCHNEIDER, 1966). The genus is also found in the locality "Dytiko-3" (DKO) of the Axios valley which has been referred to as *Hystrix* sp. (BONIS et al., 1986). The species is known from Yugoslavia, Poland, France, Spain, Bulgaria and Asia Minor (SEN et al., 1987). The age of all these faunas seems to be Turolian or Ruscinian. The Samos material comes from old collections and bears no locality indications. Thus it is impossible to say if it comes from the older level (early Turolian) or from the younger one (late Turolian). The younger records of *H. primigenia* are those from Perpignan (DEPERET, 1890), Layna and Villaroya (AGUSTI et al., 1987) indicating a Ruscinian age. Thus *H. primigenia* has a stratigraphical range from the late Miocene to Pliocene.

The species *H. major* was first described from the Quaternary of France (GERVAIS, 1859; HARLE, 1910). Later it was found in the late Villafranchian of Italy (BOSCO, 1898) and recently in the Biharian (late Villafranchian) of Spain (AGUSTI et al., 1987). The fauna of Gerakarou, from which the material studied comes, indicates a late Villafranchian (Biharian) age (KOUFOS & MELENTIS, 1983; KOUFOS et al., 1988). Thus *H. major* is a late Pliocene-Early Pleistocene species.

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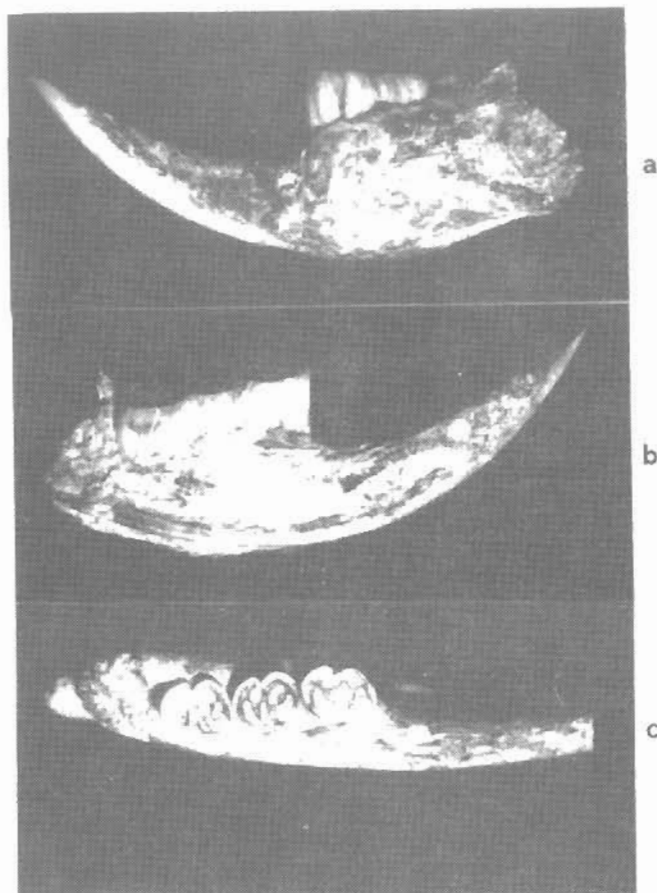
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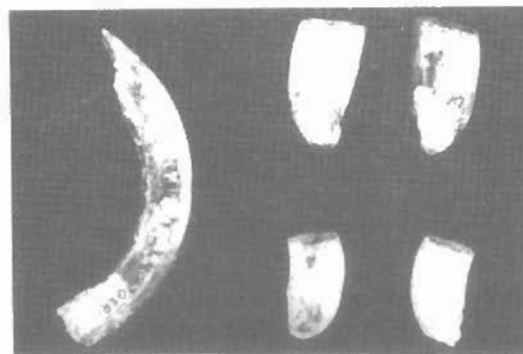
PLATE - 1

Fig. 1. *Hystrix major*. "Gerakarou-1", Macedonia, Greece.
Left mandibular ramus with I and P/4 - M/2, GER-170;
a. buccal b. lingual and c. occlusal view.

Fig. 2. *Hystrix major*. "Gerakarou-1", Macedonia, Greece;
a. Upper incisor, GER-171; lingual view.
b. Upper fourth premolar, GER-172, GER-173; lateral view.
c. Upper third molar, GER-174, GER-175; lateral view.



1



2

0 1 2 cm