

HYSTRIX REFOSSA GERVAIS, 1852 FROM PIRRO NORD (EARLY PLEISTOCENE, SOUTHERN ITALY)

LORENZO ROOK¹ & RAFFAELE SARDELLA²

Received: January 4, 2005; accepted: March 24, 2005

Key words: *Hystrix*, dentition, postcranium, Pirro Nord, Early Pleistocene, Italy

Abstract. We describe fossil remains attributable to genus *Hystrix*, collected from fissure fillings in the area between Apricena and Poggio Imperiale (Apulia, Italy). The vertebrate assemblage that yielded these *Hystrix* remains is known in the literature as Pirro Nord, and is one of the richest Early Pleistocene mammal assemblages from Italy. The porcupine remains from Pirro Nord are attributed to the species *Hystrix refoffa*. The problem of the taxonomy of Plio-Pleistocene hystricids in the framework of their morphological variability is discussed.

Riassunto. Vengono descritti resti fossili attribuibili al genere *Hystrix*, provenienti da riempimenti di fessure carsiche nell'area compresa tra Apricena e Poggio Imperiale (Gargano, Puglia). L'associazione a vertebrati che ha restituito questi resti fossili di istrice è nota in letteratura come "Pirro Nord", e costituisce una delle più ricche associazioni a mammiferi del Pleistocene Inferiore Italiano. I resti di istrice sono attribuiti alla specie *Hystrix refoffa* Gervais, 1852. Viene infine discusso il problema della tassonomia delle forme plio-pleistoceniche nel quadro della variabilità morfologica del pattern oclusale della dentatura.

Introduction

Fossil porcupines are relatively common in the European fossil record even if this taxon is considered rare. The genus is represented by different species in Europe from the Vallesian (Late Miocene; MN 10 in the European mammal biochronology) and is still living in Central and Southern Italy. It is not clear if the modern occurrence is natural or instead if it is due to re-introduction in Roman times.

The taxonomy of fossil Hystricidae is debated. In fact, the great intraspecific variability in shape, size and

enamel pattern of the occlusal surfaces make biometric and morphological comparison uncertain, in cases where the stage of attrition is not indicated. It has in fact been demonstrated that the size and occlusal surfaces are a function of the stage of attrition (Weers 1990). These characteristics, in addition to the extreme conservatism of the hystricid dental pattern, are responsible for some confusion in the taxonomy of fossil forms in this group.

Only recently, has a system of wear categories been developed for the study of molars in extant and fossil *Hystrix* (Weers 1990, 1994). The use of this system provides a useful way to avoid the confusion derived from the ontogenetic morphological changes observed in *Hystrix* teeth (cf. Weers 1985, 1994, 1995; Weers & Montoya 1996; Weers & Zheng Shaohu 1998; Weers & Rook 2003).

Aim of the present paper is to describe the *Hystrix refoffa* material from the latest Villafranchian fissure fillings of Pirro Nord (Early Pleistocene, Southern Italy) and to discuss these finds in the framework of the Italian record of the genus *Hystrix* during late Villafranchian times.

The species *Hystrix refoffa* is based on a right mandibular fragment with P₄ and alveolus of M₁, from the alluvial sediments of Perrier Hill, in the Issoire Valley, France (Gervais 1852). The holotype is kept in the Muséum National d'Histoire Naturelle in Paris, labelled with the number 109. Recently Weers (1994) provided a revision of the European Plio-Pleistocene record of this species and, in describing the topotype material stored in the "Bravard Collection" of the Natural History Museum (London), clarified the taxonomic and

1 Dipartimento di Scienze della Terra, Università di Firenze, via G. La Pira, 4 - 50121 Firenze. E-mail: lorenzo.rook@unifi.it

2 Dipartimento di Scienze della Terra, Università "La Sapienza" di Roma, P.le A. Moro, 5 - 00185 Roma. E-mail: raffaele.sardella@uniroma1.it

nomenclatural status of this species. The species has been described from the fossil record under different names – *Hystrix major* Gervais, 1859 and *Hystrix etrusca* Bosco, 1899 – that many authors have considered synonymous (Viret 1954; Chaline 1972; Agusti et al. 1987; Koliadimou & Koufos 1991; Masini & Rook 1993). More recently, Azzaroli (1998) re-described the Upper Valdarno *Hystrix* specimens and referred them to *Hystrix etrusca* without any mention of Gervais' (1852) species. The two specimens from Upper Valdarno originally described by Bosco in 1899 and currently housed at the "Museo dell'Accademia Valdarnese del Poggio" in Monteverchi (Arezzo) are well preserved. One of the two specimens is dorso-ventrally compressed and is incomplete in the nasal region, while the second is laterally compressed and lacks the occipital area. The relatively good preservation of these specimens allows recognition of traits that definitely include the species in *Hystrix* sensu stricto (Weers 1994), while tooth dimensions and proportions shows that *H. etrusca* is a junior synonym of *Hystrix refossa*.

The Pirro Nord Faunal assemblage

The fossiliferous localities known in the literature as Cava Dell'Erba and Cava Pirro are situated near Apricena (Foggia province, Apulia, Southern Italy) on the northwestern slopes of the Gargano promontory. Early Pleistocene mammals from fissure fillings in the surroundings of Apricena have been collected since the late 1960s (Pieri collection, University of Bari) and reported since the 1970s/1980s (Freudenthal 1971; De Beaumont 1979; De Giuli & Torre 1984; De Giuli et al. 1987). The Pleistocene fossil assemblage to which the materials here described belong, consists of several mammals, birds, reptiles, amphibians and rare fishes from the sandy-clayey fillings of a karst network developed along the contact between a Mesozoic and a Pliocene succession. The fossil remains have been sampled during systematic field research led by Florence and Roma "La Sapienza" Universities and belongs to different karst fissures of two adjacent quarries. Samples labelled PN (Pirro Nord) were excavated in the years 1983 to 1986 and those labelled DE (Dell'Erba) or "Stimolo" in 1991 to 1993. During the first period of field work, each fissure was sampled without recording any stratigraphic detail, whereas in the last period each level of a single fissure was sampled independently. As there is evidence that the fissures were filled in a brief time span, all the material is considered to be roughly geologically contemporaneous (Abbazzi et al. 1996).

Vertebrates (mammals, herpetofauna and birds) has been the more extensively studied group both from a taxonomic and biochronologic point of view (De Giu-

li & Torre 1984; De Giuli et al. 1987; Masini & Santini 1991; Rook 1994; Rook & Torre 1996; Abbazzi & Masini 1997; Delfino & Bailon 2000; Bedetti 2003; Pavia & Bedetti 2004; Rook et al. 2004). An interesting feature of the mammal fauna is the contemporaneous presence of taxa typical of the Faunal Unit Farneta (Gliozzi et al. 1997) associated with new forms. Remarkable is, among others, the occurrence of *Eobison*, an ovibovine related to the musk ox, the horse *Equus altidens*, an advanced form of the fallow deer *Pseudodama*, a deer close to *Megaceroides solilhacus* and the arvicolid *Microtus* cf. *M. (Allophaiomys) ruffoi*. The late Villafranchian elements of the mammal fauna suggest a Early Pleistocene age, probably preceding the Jaramillo sub-magneto-chrone as is also evidenced by the geomagnetic polarity of the sediments (Napoleone et al. 2003). The Pirro Nord assemblages are characterized by the occurrence of the vole *Allophaiomys ruffoi*, a species in Europe marking a biochronological unit in the Early Pleistocene (Late Villafranchian/Early Biharian), the "*Mimomys savini* - *Mimomys pusillus* zone", in the range of approx 1.6-1.2 Ma (Maul et al. 1998). The fossil assemblage is considered to be one of the last Italian faunas of the late Villafranchian, and Cava Pirro has been designated as the type locality of the Pirro Faunal Unit (Gliozzi et al. 1997).

The *Hystrix refossa* from Pirro

Not all the *Hystrix* material from "Pirro Nord" has been available for the present study. Fossils from Pirro Nord are stored in various institutions, following the field work activities of different researchers. Fossil mammals from Pirro Nord are kept, in addition to the Florence and Rome "La Sapienza" Universities (UF and MGPU TVp respectively), at the University of Bari and at the National Museum of Natural History (Leiden, The Netherlands). *Hystrix* remains kept in the Leiden National Museum are discussed by Weers (1994).

The sample available is the result of several field surveys carried out in the area between Apricena and Poggio Imperiale by researchers from the Florence and Rome "La Sapienza" Universities. Fossils from the earliest collections, kept in Bari, have been in part available for this study (specimens identified by the acronyms "PP" or "GP").

The Pirro Nord *Hystrix* sample available for this study consists of 53 remains. Elements of the postcranium are represented (humerus, radius, ulna, femur, tibia, astragalus, calcaneum and metapodials), but craniodental remains (especially teeth) are more abundant. Represented in the sample are isolated incisors, some mandibular elements (two almost complete mandibles) and nineteen isolated teeth. The tooth wear stages are

indicated according the wear classification proposed by Weers (1990) and range from A (unworn) to H (deeply worn) for upper teeth and O (unworn) to T (deeply worn) for lower teeth.

Material

Upper dentition. UF DE2d/551, fragmentary left upper incisor; UF DE12-2/nn (9.2.92), fragmentary left upper incisor; UF P79-1/nn, Left P⁴ (Fig. 1i-l) wear stage “B”; MGPUtVp 1542, right P⁴ wear stage “D”; MGPUtVp 1543, left P⁴ wear stage “B?”; UF DE2d/47, left M^{1/2} wear stage “C”; UF PN34a/nn (29.6.86), left M^{1/2} (Fig. 1 q-s) wear stage “D”; UF DE2d/176, right M^{1/2} wear stage “G”; UF DE12-1/nn, left M^{1/2} (Fig. 1 m-p) wear stage “G”; UF PN6/nn, left M^{1/2} (Fig. 1 e-h) wear stage “C”; MGPUtVp 1544, left M^{1/2} wear stage “F”; UF PN11/nn, right M³(?) (Fig. 1 a-d) wear stage “G”; MGPUtVp 1545, left M³ wear stage “C/D”; MGPUtVp 1546, left M³ wear stage “D”; MGPUtVp 1547, right M³ wear stage “F”.

Lower dentition. UF PN11/nn, right mandible with P₄-M₃ (Fig. 2 a-d) wear stages: P₄ = “S”, M₁, M₂ and M₃ = “T”; UF DE1/nn (1991), right mandible with P₄-M₃ (Fig. 2 e-h) wear stages: P₄ = “O”, M₁ and M₂ = “S”, M₃ = “Q”; UF PN5/nn, left fragmentary mandible with M₁-M₃ (Fig. 2 i-k) wear stage: M₁ = “O”, M₂ = “O” and M₃ = “O”; UF Stimolo alto (27.5.92), right fragmentary mandible with P₄ (wear stage “P”) and I alveolus; UF P73-1/nn, edentulous right mandible fragment; UF DE6-4/nn (1.9.91), right mandible fragment with M₁ wear stage “T”; UF PN34b/nn (29.6.86), fragmentary right lower incisor; UF DE2d/234, fragmentary left lower incisor; UF DE2d/71, fragmentary left lower incisor; MGPUtVp nn, left lower incisor; MGPUtVp nn, left incisor fragment; UF DE6b/nn (19.9.91), enamel fragment of an incisor; UF PN34d/nn (30.6.86), fragmentary

left lower incisor; UF PN4/nn, left lower incisor; UF PN4/nn, extremely worn right M₁ (Fig. 3 a-b) wear stage “T”; UF PN34a/nn (29.6.86), left M_{1/2} wear stage “S”; UF PN27/nn, left M₁₋₂ (Fig. 3 d-f) wear stage “T”; GP/361, left M_{1/2} (Fig. 3 g-i) wear stage “R”; GP/361, left M₃ (Fig. 3 j-l) wear stage “S”; UF DE2d/235, left DP₄ (Fig. 3 c) wear stage “T”.

Postcranial elements. UF PN27/nn, distal part of a right humerus (Fig. 4 a-b); MGPUtVp1548, right fragmentary humerus (juvenile); MGPUtVp1549, left juvenile humerus (proximal head unfused); UF PN11/nn, left radius; MGPUtVp nn, left fragmentary ulna; UF PN11/nn, distal part of a right femur (Fig. 4 k-l); UF DE4/1, proximal part of a right femur (Fig. 4 h-j); MGPUtVp nn, “right femur fragment (diaphysis and proximal end; juvenile); MGPUtVp nn, left femur fragment (diaphysis and proximal end; juvenile); MGPUtVp nn, left femur fragment (proximal end; juvenile); PP/384, right tibia (Fig. 4 m-n); PP/349, left tibia (juvenile) (Fig. 4 o-p); UF PN34a/nn (29.6.86), right astragalus (Fig. 4 f-g); MGPUtVp nn, left astragalus; UF P79-1/nn, left calcaneum (Fig. 4 c-e); UF PN5/nn, right metacarpal V(?); UF PN2c/nn, metacarpal; UF DE2d/291, left metatarsal IV (?).

Description and comparisons

All the specimens are well preserved and morphological details are easily seen in each specimen. Few remains (only three) are affected by a certain degree of abrasion due to transport and/or old fractures, i.e. made during phases of the biostratigraphic process before recovery. Such specimens are a distal portion of a right humerus (PN27/nn; Fig. 4 a-b), a lower molar (PN34a/nn 29.6.86) and the fragmentary mandible from the

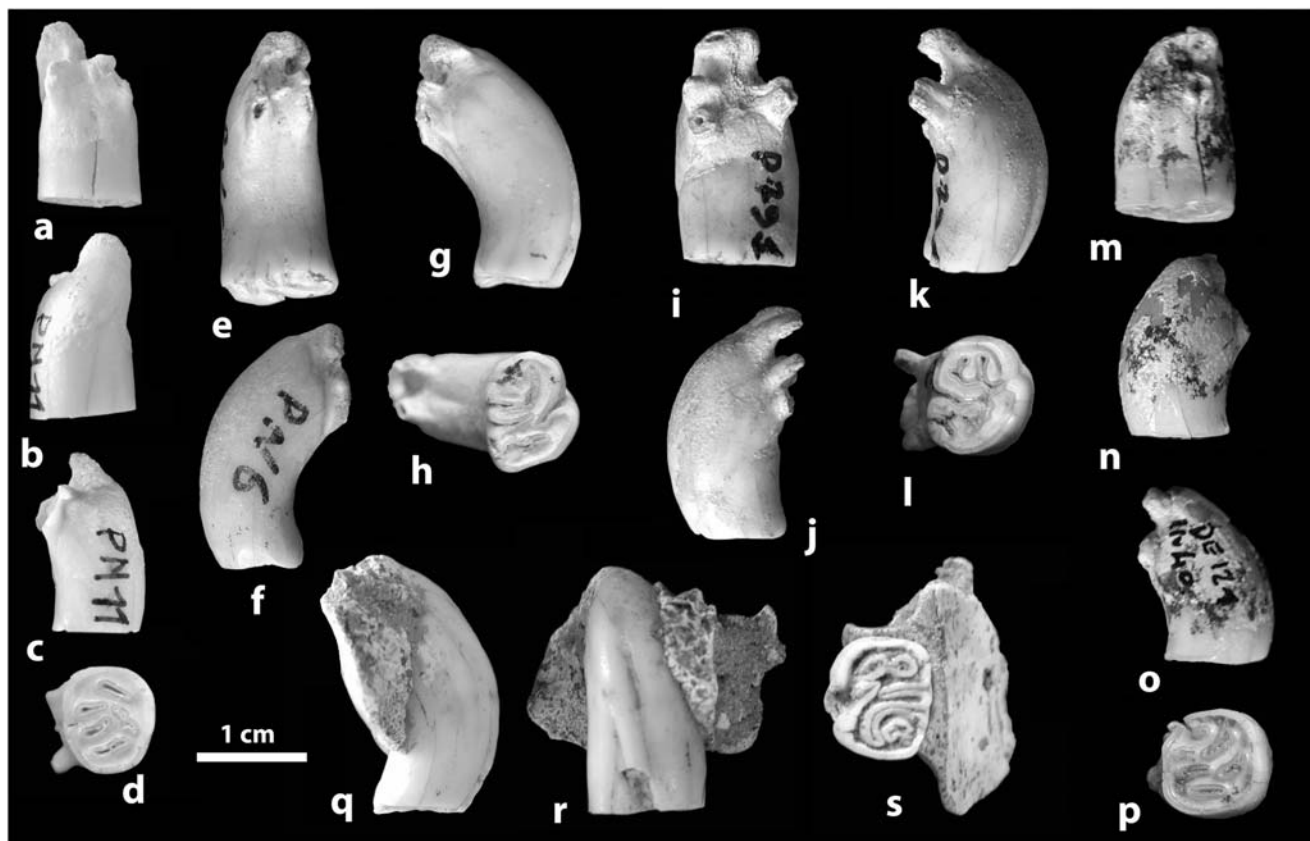


Fig. 1 - *Hystrix refossa* from Pirro Nord: upper teeth. a-d) PN11/nn, right M³(?); e-h) PN6/nn, left M^{1/2}; i-l) P79-1/nn, left P⁴; m-p) DE12-1/nn, left M^{1/2}; q-s) PN34a/nn (29.6.86), left M^{1/2}.

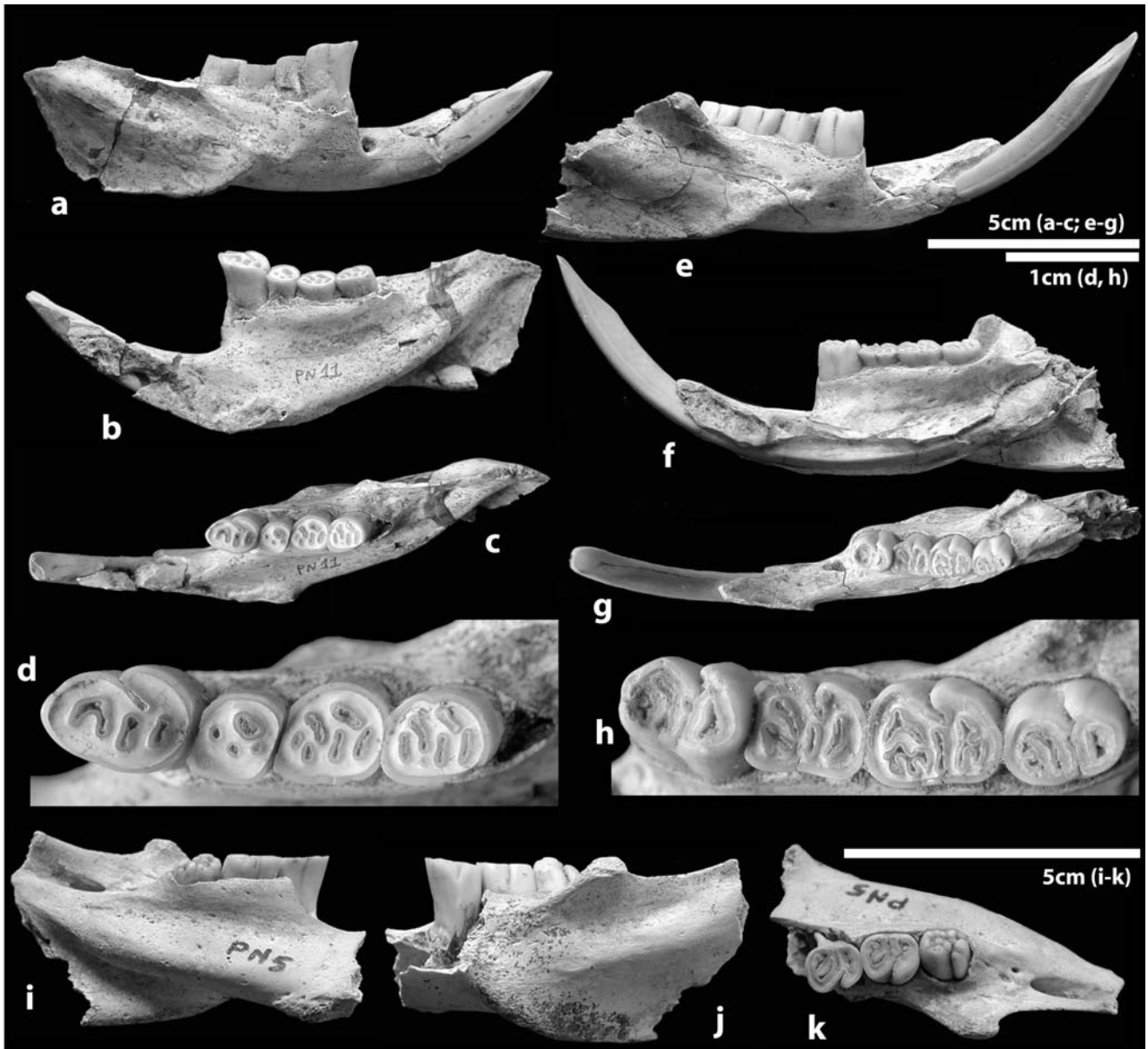


Fig. 2 - *Hystrix refossa* from Pirro Nord: mandibles. a-d) PN11/nn, right mandible with P₄-M₃; e-h) DE1/nn (1991), right mandible with P₄-M₃; i-k) PN5/nn, left fragmentary mandible with M₁-M₃.

quarry “Stimolo alto” (labelled “27.5.92”). All the remaining fossils have unweathered surfaces and, if fractures are present, these are “fresh” and thus linked to the quarrying activities that brought to light the karst fissures and their fossiliferous content.

Notable elements in the collection are two almost complete mandibles: specimen PN11/nn (Fig. 2a-d) and specimen DE1/nn (Fig. 2e-h). Notwithstanding a few small fractures, both specimens preserve the entire mandibular body (both lack the ascending ramus) and the strong lower incisor in its alveolus. The tooth-row is complete in both specimens and allows us to interpret the first individual (PN 11/n) as an adult one (very advanced dental wear, stages “S”-“T”; Fig. 2d) and the second one (DE1/nn) as a much younger individual

(wear stages “O” for P₄, “S” for M₁ and M₂, and “Q” for M₃). The latter mandible bears a P₄ (the last tooth emerging and beginning to wear very late in the life of the individual) with an occlusal surface at a very early stage of wear, “O” (Fig. 2h).

Comparative analyses have mainly focus on tooth dimensions and proportions. A first note concerns the absolute size. All elements (upper and lower P₄, M₁ and M₂) of the Pirro Nord *Hystrix* considered here are basically larger than extant *H. cristata* (Fig. 5 and 6), as is generally true for the fossil species *Hystrix refossa*. Compared with fossil European species, the Pirro Nord form is clearly larger than the very small-sized Late Miocene species *Hystrix parvae*, while is comparable in size to the Mio-Pliocene *H. primigenia* and *H. deper-*

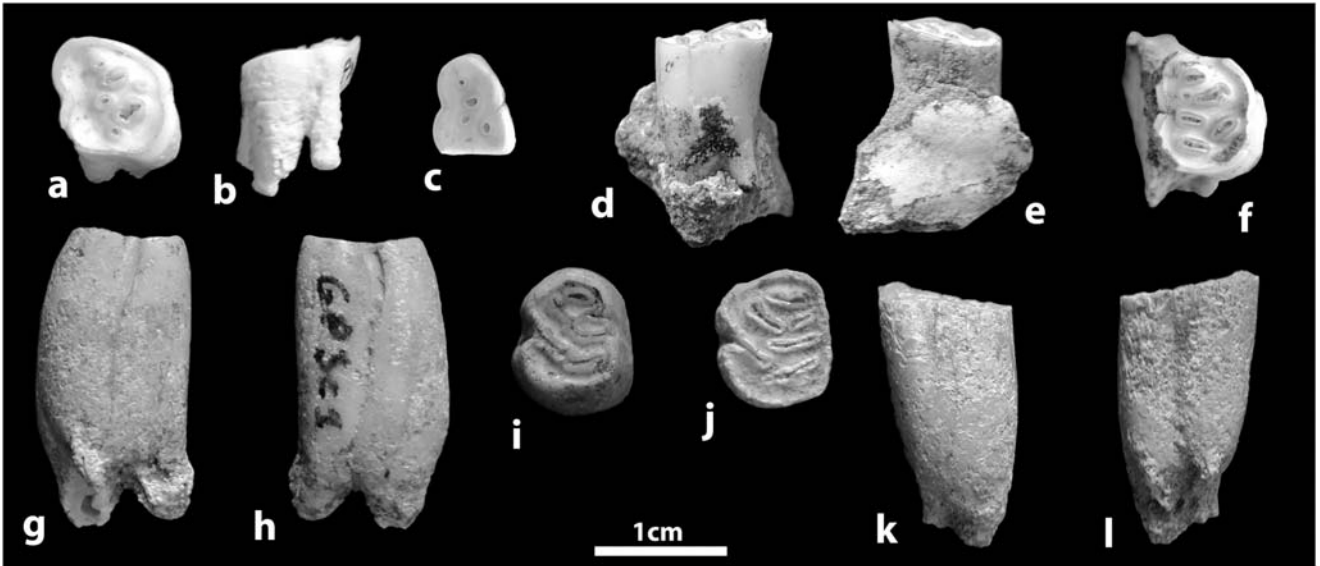


Fig. 3 - *Hystrix refossa* from Pirro Nord: lower teeth. a-b) PN4/nn, right M₁; c) DE2d/235, left DP₄; d-f) DE6-4/nn, right M₁; g-i) GP/361, left M_{1/2}; j-l) GP/361, left M₃.



Fig. 4 - *Hystrix refossa* from Pirro Nord: postcranial bones. a-b) PN27/nn, distal portion of a right humerus; c-e) P79-1/nn, left calcaneum; f-g) PN34a/nn (29.6.86), right astragalus; h-j) DE4/1, proximal portion of a right femur; k-l) PN11/nn, distal portion of a right femur; m-n) PP/384, right tibia; o-p) PP/349, left tibia (juvenile);

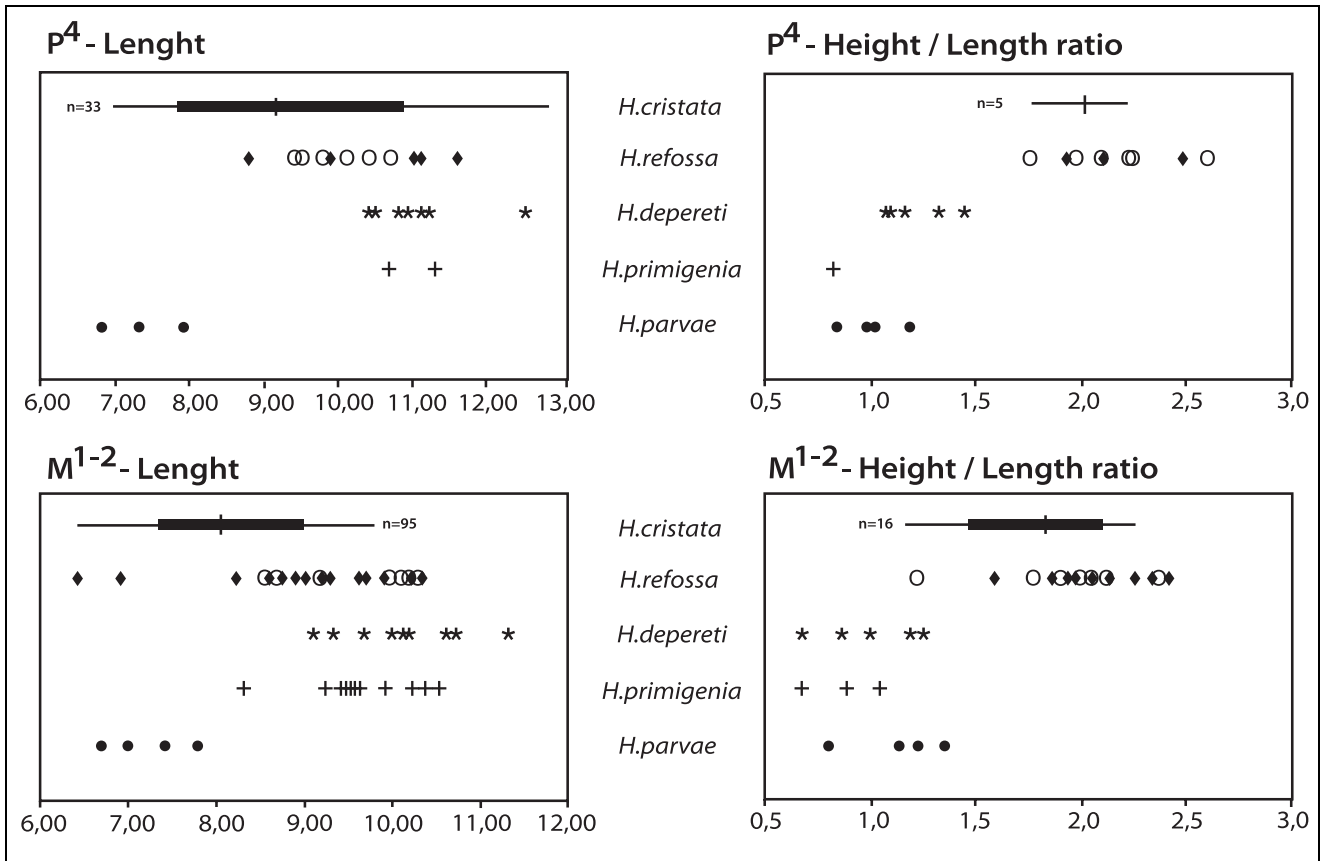


Fig. 5 - Upper dentition (P^4 and M^{1-2}) graphs showing the range of occlusal length (left column) and hypsodonty index (length/crown height; right column) for different Miocene to Pleistocene *Hystrix* species. *Hystrix refossa* specimens from Pirro Nord are indicated by open circles. Comparative data from van Weers (1994), van Weers & Montoya (1996), van Weers & Rook (2003).

eti (Pikermi, Perpignan etc.) and to the Plio-Pleistocene species *H. refossa* (Ostramos-8, Upper Valdarno, St. Vallier, Perrier, Venta Micenea etc.).

When instead the crown height/tooth length ratio is considered (Fig. 5 and 6), the picture that emerges is quite interesting. The Pirro Nord *Hystrix* appears characterised by a relatively high degree of hypsodonty, similar to the extant *H. cristata* (despite the few data available for upper and lower P^4 ch/tl ratios), and to that of the Plio-Pleistocene species *H. refossa*. The two Mio-Pliocene species (*H. primigenia* and *H. depereti*), although comparable in size, show a very low hypsodonty index, similar to that of the very small-sized *Hystrix parvae*.

As already stressed by Weers (1994) and Weers & Rook (2003), a distinctive trait in *Hystrix* evolution is the development of hypsodont taxa from the Mio-Pliocene ones to the later Plio-Pleistocene and Extant species.

Discussion and conclusions

It is here worth stressing the taxonomic implications already suggested by van Weers (1994) and reinforced by Weers & Rook (2003) in considering *Hystrix*

refossa a valid species including a number of species named on material from several Plio-Pleistocene localities in Europe (*H. majori*, *H. etrusca*) Near East (*H. angressi*) and Africa (*H. makapanensis*). All of these are based on morphological details of the dentition known to be an expression of variability in occlusal morphology.

Functionally, the acquisition of a high crowned dentition is relatively easy to understand, while the causal reason behind these evolutionary changes is not so clear. As a matter of fact, the Plio-Pleistocene transition was matched by dramatic changes in continental mammal assemblages in connection with climatic and environmental changes that were forerunners of the later and more intense phases of the glacial Quaternary.

The disappearance of wooded landscapes and expansion of more open habitats drove the evolutionary patterns and feeding/locomotor adaptations of several mammal groups. Within the framework of these changing environments and landscapes, the genus *Hystrix* developed the observed high degree of hypsodonty.

Besides the highcrowned dentition, the Plio-Pleistocene *H. refossa* is characterized by another morphological peculiarity. All known postcranial elements are stoutly built and characterized by their notable size.

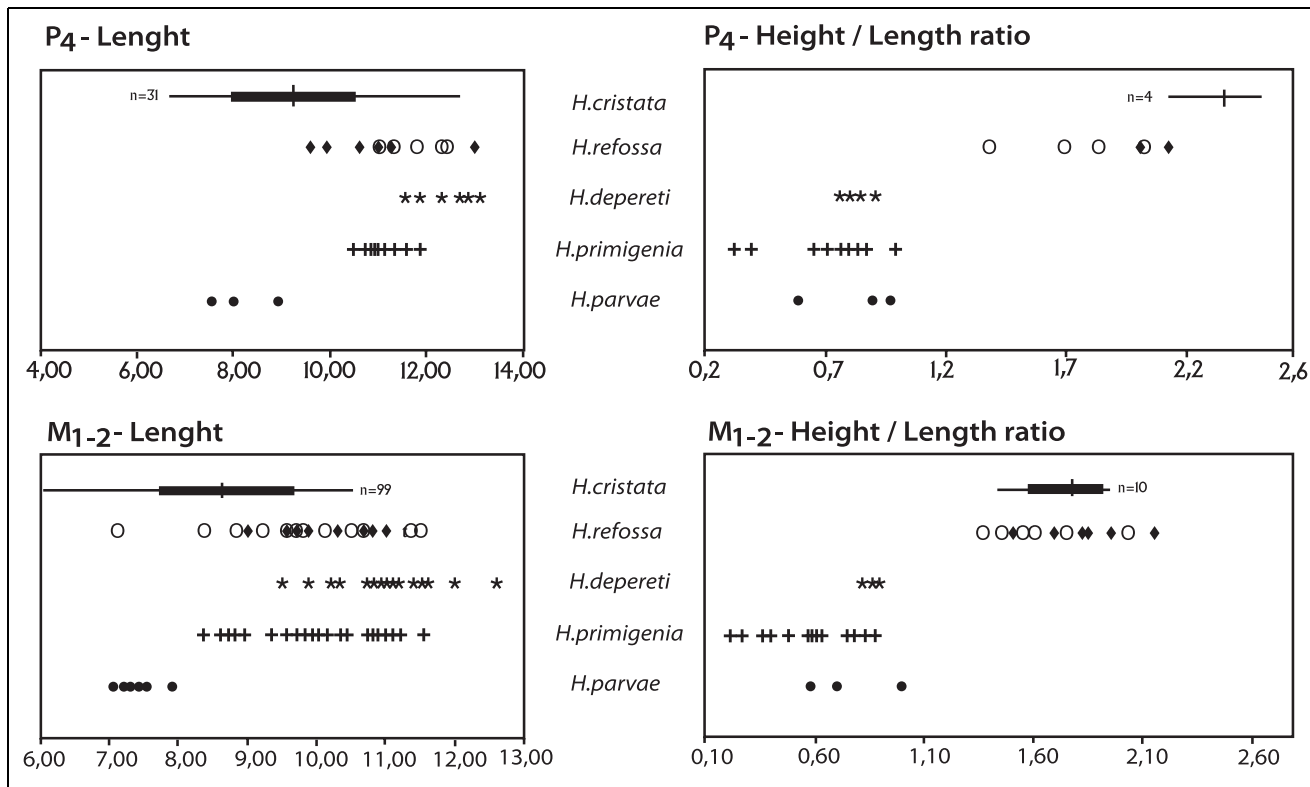


Fig. 6 - Lower dentition (P_4 and M_{1-2}) graphs showing the range of occlusal length (left column) and hypsodonty index (length/crown height; right column) for different Miocene to Pleistocene *Hystrix* species. *Hystrix refossa* specimens from Pirro Nord are indicated by open circles. Comparative data from van Weers (1994), van Weers & Montoya (1996), van Weers & Rook (2003).

This trait was already commented in the work of early paleontologists such as Gervais (1869) and Deperét (1890), both stressing the large postcranial skeleton of the species “*H. major*”. The Pirro Nord sample provides extensive evidence that the postcranial skeleton of Plio-Pleistocene *Hystrix refossa* was really larger and stouter compared to the late Miocene *H. primigenia* and *H. depereti*, thus showing a different adaptation, perhaps linked to a dryer and/or cooler environment.

These peculiar adaptations, readily observable in the Pirro Nord porcupine, confirms a peculiar environmental picture emerging from other taxa. Recent studies on the extremely well documented and rich bird com-

munity (Bedetti 2003; Pavia & Bedetti 2004) demonstrated that the environment recorded for the Pirro Nord area was characterized by a predominantly dry and open landscape. This is confirmed by the recent demonstration of the occurrence of a cercopithecoid primate attributable to the genus *Theropithecus* (the Gelada baboon; Rook et al. 2004).

Acknowledgments. The senior author deeply appreciates the opportunity to interact with Dees van Weers (Zuilichem), for his deep knowledge of extant and fossil Hystricidae, and especially for his kind friendship. We thank E. Di Canzio (Rome) for assistance in locating the Pirro specimen kept in the Rome “La Sapienza” collection. The work was supported by the University of Florence (Fondi d’Ateneo) grants.

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