OLD WORLD PORCUPINE (RODENTIA, HYSTRICIDAE) REMAINS FROM THE LATE MESSINIAN OF PIEDMONT, NW ITALY

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Abstract. The goal of this paper is to describe a single upper molar and a fragmented radius of Old World porcupines recently discovered in the latest Messinian localities of Moncucco Torinese and Verduno in the Tertiary Piedmont Basin, NW Italy. The available material can be assigned to the large-sized species *Hystrix (Hystrix) depereti*, rarely found in the late Turolian and early Ruscinian of Europe. A combined comparative and morphofunctional analysis of the fragmented radius suggest that *Hystrix (Hystrix) depereti* was characterized by a generalized terrestrial locomotory behaviour thus being very similar to extant Old World porcupines. Paleobiogeography and paleoecological consequences are also discussed.

Introduction

Diverse fossil assemblages consisting in both vertebrate and invertebrate remains have been described in the last few years from the latest Messinian continental deposits exposed at Moncucco Torinese and Verduno (Sardella 2008; Angelone et al. 2011; Colombero & Pavia 2013; Colombero et al. 2013, 2014a, 2014b; Harzhauser et al. in press). Up to date, the Italian record of Miocene terrestrial vertebrates is primarily represented by the endemic faunal assemblages of the Tusco-Sardinian and Apulo-Abruzzi paleobioprovinces (e.g., Freudenthal 1971; Rook et al. 2004, 2006, 2011; Rinaldi & Masini 2009; Patacca et al. 2013; Villier & Carnevale 2013; Villier et al. 2013; Savorelli et al. in press). Conversely, non-endemic continental vertebrate assemblages are very rare in the Italian Miocene record. During the Messinian, vertebrate taxa from Europe dispersed into the emerging Italian peninsula as evidenced by certain fossil assemblages of Central and NW Italy

(Rook et al. 2006). In Piedmont (NW Italy), Moncucco Torinese and Verduno constitute the most productive sites (Sardella 2008; Angelone et al. 2011; Colombero & Pavia 2013; Colombero et al. 2013, 2014a, 2014b; Alba et al. 2014a). Overall, these two localities comprise 15 rodent taxa, six of which recognized at Verduno and 13 in the highly diverse assemblage of Moncucco Torinese. The compositional differences are possibly related to different palaeoecological and/or palaeobiogeographical contexts, and/or to different taphonomic processes that controlled the accumulation of fossil remains (Colombero & Pavia 2013; Colombero et al. 2013, 2014a, 2014b; Harzhauser et al. 2015). In this paper, we will focus on material belonging to large sized rodents of the family Hystricidae, the Old World porcupines, previously unknown in the Miocene of Piedmont.

Old World porcupine remains from the Miocene of Italy are extremely rare, being up to date solely represented by *Hystrix depereti* from the late Messinian (late Turolian, MN 13) of Brisighella (Masini & Rook 1993; Weers & Rook 2003). Few remains of undetermined hystricids are reported in the Late Pliocene (early Villanyian MN 16a) of Arondelli (Piedmont) and Barga (Tuscany) (Berzi et al. 1967; Kotsakis 1986). In the Late Pliocene (late Villanyian MN 16b) and, subsequently, in the Early Pleistocene (early Biharian), *Hystrix refossa* has been commonly reported from several Italian localities (Kotsakis et al. 2003). This species is particularly abundant in the locality of Pirro Nord (Rook & Sardella 2005, 2013; Pavia et al. 2012; Alba et al. 2014b). During the Middle and Late Pleistocene (early and late Toringian) the small species *Hystrix (Acanthion) vinogradovi* was reported in few Northern and Central Italian local-

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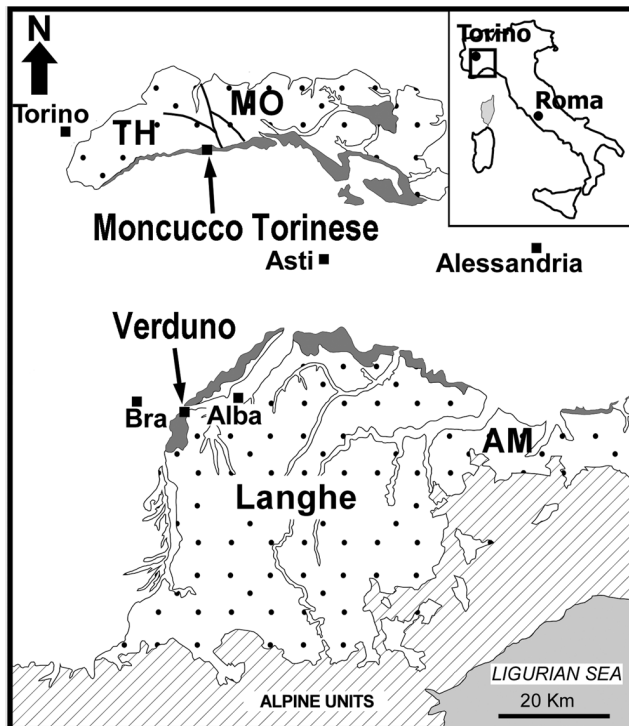
Fig. 1   - Geographic and stratigraphic setting of the Tertiary Pied-
mont Basin (TPB). White area: Pliocene-to recent depos-
its; dark grey area: Messinian deposits; dotted area: Eo-
cene-to-Tortonian deposits; dashed area: Alpine sectors;
light grey: Ligurian Sea. The arrows indicate the geo-
graphic positions of the two fossiliferous sites Moncucco
Torinese (MCC) and Verduno (VRD). TH: Torino Hill;
MO: Monferrato Hills; AM: Alto Monferrato. Modified
from Lozar et al. (2014).

ities (Kotsakis et al. 2003; Salari & Sardella 2009). Fi-
nally, the Italian territory is currently the only Eur-
opean area where a porcupine is commonly present.
Indeed, the crested porcupine *Hystrix cristata* is a com-
mon element of the Apennine fauna (Santini 1980).
However, even if the genus *Hystrix* was widely distrib-
uted in Europe during the Pleistocene, there is no evi-
dence of the presence of European Old World porcu-
pines during the Holocene. The antropochorous origin
of the Italian Old World porcupine populations is cur-
rently accepted, resulted from several introductions in
historical (probably since Late Antique/Early Medieval
period) and more recent periods mainly for edible, ve-
natory and even supposed para-pharmaceutical pur-
poses (Masseti et al. 2010; Mori et al. 2013). The geo-
graphical range of this taxon is currently increasing and
now includes some districts of southern Piedmont and
the Po Valley (Mori et al. 2013; Dutto et al. 2014).

Locality

The fossils documented herein come from two
latest Messinian localities of Piedmont, NW Italy, Mon-

cucco Torinese and Verduno. The stratigraphy of the
fossiliferous deposits has been extensively discussed in
recent papers (Colombero et al. 2014a; 2014b). In sum-
mary, the vertebrate fossils of Moncucco Torinese and
Verduno are roughly coeval in age and can be referred
to the post-evaporitic phase of the Messinian Salinity
Crisis between 5.55 and 5.33 Ma (Dela Pierre et al.
2007; 2011). However, biostratigraphical data indicate
that the investigated succession of Moncucco Torinese
has an age that cannot be older than 5.41 Ma (Alba et al.
2014), correlatable with the stage 3.2 of the Messinian
Salinity Crisis (sensu Roveri et al. 2014). Preliminary
stratigraphic analyses seem to indicate that the fossil
vertebrates from Verduno occur close to the base of
the post-evaporitic succession and are therefore corre-
latable with the stage 3.1 of the MSC, between 5.55 and
5.41 Ma (Dela Pierre et al. 2014).

Material and methods

The material described herein consists of a single tooth that was
collected from a conglomeratic layer (layer VRD 5 of Colombero et al.
2013, 2014b) at Verduno, and in a proximal fragment of right radius
that has been recovered at Moncucco Torinese in the layer MCC4
(Colombero et al. 2014a). Several dental and postcranial remains per-
taining to individuals of *Hystrix refossa* from the Early Pleistocene
locality of Pirro Nord, plus those of a single individual of extant crested
porcupine *Hystrix cristata* were used for comparative purposes. The
studied radius was also compared with forelimb skeletal elements of
extant medium-to-large-sized rodents, Alpine marmot *Marmota mar-
mota* and Eurasian beaver *Castor fiber*. The taxonomy of the fossil
species of *Hystrix* is rather complex due to the plethora of species that
are based on scarce or inadequately preserved material. For this reason,
the taxonomy followed in this paper is based on the revisionary studies
of the genus published by Weers & Rook (2003), Weers (2004, 2005)
and Sen & Purabrishemi (2010) unless otherwise indicated. The nomen-
clature of dental features mostly follows that of Montoya (1993) and
Sen (2001a) (see Fig. 2); the osteological nomenclature follows that of
Dunn & Rasmussen (2007) and Candela & Picasso (2008). Measure-
ments of tooth (Fig. 2) and classification of the wear stage of the tooth
follows Sulimski (1960), Weers (1990) and Weers & Montoya (1996). In
particular, the EH (enamel height) represents the distance between the
occlusal surface and the base of the enamel on the lingual side; the EH/
L ratio is useful to evidence the hypsodonty in detached teeth within
species of different size (see Fig. 2). The wear stages are classified
following Weers (1990) and Weers & Rook (2003) and indicated by
capital letters from A (unworn tooth) to H (deeply worn teeth) in
upper molars and from O to T in lower molars. We also calculate the
distance between the sinus (=hypoflexus) and the base of the crown
(Hs: height of the sinus); this value has been measured with the same
methodology of the EH (Weers & Montoya 1996) in order to quantify
along the lingual side and the distance between the base of the hypo-
flexus (or sinus) and the base of the enamel crown, defined by the plane
parallel to the occlusal surface of the tooth (Fig. 2). Hs has been for-
mally calculated only for the Asiatic taxa *H. gansuensis* and *H. lufen-
gensis* (Wang & Qiu 2002; Wang & Qi 2005) whereas it has been
indicatively reported for European taxa for the P4 of selected species
(Lopatin et al. 2003) or for some upper molars of *Hystrix primigenia*
and *Hystrix depereti* (Sen 2001a). The distance between the base of the
hypoflexus and the occlusal surface is the depth of the sinus (Ds).
However, this parameter is strongly influenced by the wear stages of

the analyzed specimens. Measurements of the radii follows Driesch (1976). Measurements and photographs of the tooth have been taken with the digital measurement tool of the Leica Application Suite V. 3.3, whereas a digital caliper and a Canon 5D digital camera were used for the radii. Tooth morphology has been diagrammatically reconstructed using a Wild M5A stereo-microscope equipped with a camera lucida drawing arm. The fossil material is currently housed in the Museo di Geologia e Paleontologia of the Università degli Studi di Torino (MGPT-PU), while the recent comparative material is housed in the Dipartimento di Studi Umanistici of the Università degli Studi di Ferrara.
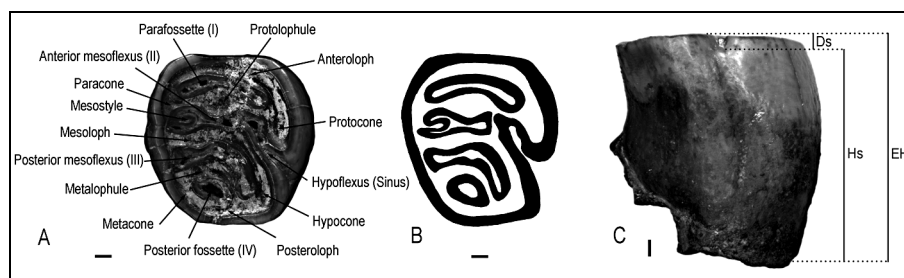

Fig. 2 - Right M1/2 (MGPT-PU128348) of *Hystrix depereti* Sen, 2001 from the Late Miocene, late Messinian (late Turolian, MN 13) of Verduno, Piedmont, Italy: A. - Occlusial view; B - Diagram of the occlusal surface; C - Anterolingual view, also illustrating the measurement methodology. The nomenclature follows Sen (2001a); the numbering of the synclines according to Montoya (1993) is indicated in the brackets; Ds: Depth of the sinus; Hs: distance between the hypoflexus (sinus) and the crown-base on the lingual side (see text for details); EH: enamel height on the lingual side. Scale bars: 1 mm.

Systematic Paleontology

Family Rodentia Bowdich, 1821

Family Hystricidae Fischer von Waldheim, 1817

Genus *Hystrix* Linnaeus, 1758

Subgenus *Hystrix* Linnaeus, 1758

Hystrix (Hystrix) depereti Sen, 2001

Fig. 2A-C; Fig. 3A

Type locality: Serrat-d'en-Vaquer, Perpignan, Pyrénées-orientales, France, Early Pliocene (Ruscinian, MN 15).

Material: A single right M1/2 (MGPT-PU128348) from layer VRD5 of the late Messinian (late Turolian, MN 13) of Verduno, Piedmont, Italy (Colombero et al. 2013); a single proximal half of a right radius (MGPT-PU 128349) from layer MCC4 of the late Messinian (late Turolian, MN 13) of Moncucco Torinese, Piedmont, Italy (Colombero et al. 2014a).

Description

M1/2. The single M1/2 exhibits anterior and posterior wear facets. The occlusal outline is sub-quadratic. The occlusal surface displays a high degree of wearing resulting in the preservation of a single fold, the hypoflexus or lingual sinus. The other folds are reduced to enamel islets. The first enamel islet, corresponding to the parafossette, is narrow and elongated, slightly bending on the lingual side; the second enamel islet corresponds to the anterior mesoflexus; it is very close to but already separated from the hypoflexus (lingual sinus); on the labial side, it splits in two branches forming a Y-shaped structure; the area enclosed between the two branches indicates that a deep mesostyle was present in origin; the third enamel islet, the posterior mesoflexus, is strongly bended to the lingual side, enclosed between the mesoloph and the metalophule; the labial side of this enamel islet is very close to the labial wall of the tooth; the fourth enamel islet is the small posterior fossette enclosed between the metalophule and the pos-

teroloph. The tooth reveals a medium degree of hypsodonty and can be considered semi-hypsodont (sensu Sen & Purabrishemi 2010; Nishioka et al. 2011). There are three roots that are only partially preserved; on the lingual side the strongest root exhibits a narrow antero-posteriorly developed oval section; the antero-labial root is very small and rounded; the postero-labial root is slightly larger and bilobed, developing in lingual direction on the posterior side.

Radius. The distal epiphysis is totally lacking and only the proximal and medial parts of the main shaft are preserved. The structure of the bone is quite stout. The shaft is moderately twisted due to a counterclockwise torsion clearly visible in proximal view. The radial head is ovoid in proximal view, with the medial region slightly more expanded than the lateral side; the ventral border is much more rounded and convex in shape than the dorsal border; on the dorsal border a shallow incision is present slightly laterally to the capitular eminence; the capitular eminence is relatively well developed, emerging from the dorsal border of the medial part of the head; the humeral articular surface is concave in the articulatory area for the humeral capitulum (fossa of the capitulum) and it becomes convex on the medial side where it articulates with the humeral trochlea; the medial border of the head is slightly abraded due to erosion; it is gently curved medially where it articulates with the coronoid process of the ulna. The ulnar facet is well developed on the ventral side; it exhibits a sigmoid profile extending from the posterolateral facet to the medial margin. The neck is stout. A moderately developed radial bicipital tuberosity slightly protrudes laterally along the ventral side. The dorsal side presents a smooth surface. The bone-shaft is gently convex dorsally and moderately twisted; it is characterized by an ovoid section close to the neck and it becomes triangular and mediolaterally compressed at the distal end of the preserved portion. The lateral margin, or interosseus
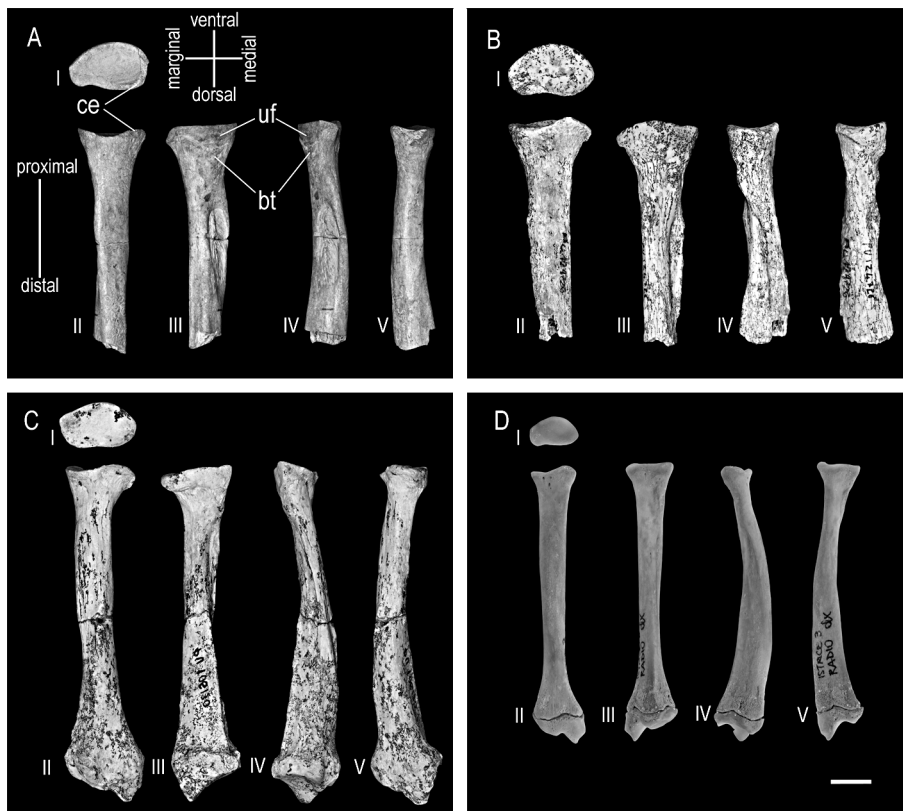
Fig. 3 - Radii of Neogene and extant *Hystrix* species in proximal (I), dorsal (II), ventral (III), marginal (IV) and medial (V) views. A - *Hystrix depereti* Sen, 2001, from the Late Miocene, late Messinian (late Turolian, MN 13) of Moncucco Torinese, Piedmont, Italy: fragment of a right radius (MGPT-PU 128349). B-C - *Hystrix refossa* Gervais 1852, from the Early Pleistocene (early Biharian) of Pirro Nord, Apulia, Italy: B) fragment of a right radius (MGPT-PU 124726); C) left (reversed) radius (MGPT-PU 105170). D) *Hystrix cristata* (Linnaeus 1758), recent, Italy: right radius of a sub-adult individual (University of Ferrara not numbered). Scale bars: 1 mm.

crest, is prominent, displaying a well-defined sharp profile that follows the slight dorsal convexity of the shaft. The medial margin is large and slightly rounded. An elliptical rugose surface for the attachment of the *membrana interossea antebrachii* is considerably developed close to the lateral margin on the ventral side of the shaft; it is wide and deep with well-developed structures for the attachment of the interosseus ligaments.

Measurements. See Tables 1 and 2.

Comparative analysis

M1/2. The single upper molar from Verduno displays a large size and the typical pentalophodont structure of the cheek teeth of Hystricidae. Within this family, only the taxa of *Hystrix* (subgenus *Hystryx*) are consistent with size of the available specimen. As previously reported (Sen 2001a), the occlusal pattern of the cheek teeth of *Hystrix* is highly conservative and therefore scarcely useful for the correct identification of the different species within the genus. Conversely, the most useful discriminative characteristics are the size and the degree of hypsodonty.

With the exception of *Hystrix parvae* and *H. vinogradovi*, all the European Neogene and Pleistocene species were rather large in size distinctly exceeding *H. cristata*. According to the degree of hypsodonty, *H. parvae*, *H. primigenia* and *H. trofimovi* display low-crowned teeth whereas *H. depereti*, *H. aryanensis*, *H.*

gansuensis H. paukensis H. caucasica, H. zhengi, with slightly higher tooth crown, are semi-hypsodont since they exhibit less hypsodont teeth than *H. refossa* and *H. vinogradovi* (Sen & Purabrishemi 2010; Nishioka et al. 2011).

Compared to the dental remains of the Neogene Asian taxa, the tooth from Verduno is smaller than those of *Hystrix paukensis*, whereas is larger than those of *H. aryanensis* (Sen 2001b; Nishioka et al. 2011; 2014). Moreover, the latter species exhibits a peculiar occlusal pattern of the upper molars in which the second buccal and the lingual folds are connected even in advanced stages of wear (Sen 2001a). The upper molars of *H. gansuensis* are slightly smaller and slightly more hypsodont compared to the specimen from Verduno. However, it is worth noting that the highest values of EH/L index in *H. gansuensis* are reported for poorly worn teeth (A-B, see Weers 2004) whereas the M1/2 from Verduno displays a more advanced stage of wear (G). Finally, the Hs calculated for some specimens of *H. gansuensis* (Wang & Qiu 2002) (Tab. 1) is slightly lower than that of the M1-2 from Verduno being comprised between the values observed for *H. primigenia* and *H. depereti* (Tab. 1). Since the teeth of *H. gansuensis* exhibit a similar or even more developed degree of hypsodonty, a lower Hs parameter suggests that this species exhibits a deeper hypoflexus than *H. depereti*. According to Weers (2005), *H. gansuensis* should be regarded as the probable ancestor of the high crowned Pleistocene *Hy-*

		H. depereti			H. primigenia		H. gansuensis	H. lufengensis	H. aryanensis		H. refossa	
		PRP	BRS	VRD	PIK	KMK	GAN	LUF	MLY	IVN	PER	PN
L	x̄	10.3	9.65	10.1	9.6	9.4	9.5	8.7	8.9	9.8	10.25	9.8
	range	9.6-10.8	9.2-10.1		9.0-10.0	9.0-9.9	8.4-10.1	7.6-9.8	8.6–9.4		10.2-10.3	8.1-10.8
W	x̄	10.0	9.5	9.3		9.9	8.9	8.8	8.5	8.8	9.25	8.8
	range	8.9-10.7	9.1-9.9		10.2-10.8	9.2-11.1	7.6-10.0	7.5-9.4	8.0–9.6		9.0-9.5	7.0-9.7
EH		10.4		12.6			12.3		11.5	9.3	20.1	18.3
	range	6.2-14.7					9.3–14		11.2–12.2		19.8-20.3	10.3-21.25
EH/L	x̄	92	123	125(F)	74	60	143	91	129	0.9	196	178.5
	range	62 (G)-120(G)	121(C)-125(D/E)		70(G)-80(F)	42(G)-68(G)	139-152(A-D)	67(E)-116(B)			194-197(C-D)	111 (G)-216(F/B)
Hs	x̄	>10.0		12.2	~7-8		9.6	6.2				17.05
	range						8.0-11.6	6.1-6.5				15.6-19.5

Tab. 1 - Measurements of M1/M2 of *Hystrix depereti* Sen 2001 from the Late Miocene, late Messinian (late Turolian, MN 13) of Verduno, Piedmont, Italy and other localities with comparisons with other Neogene species of *Hystrix* from Eurasia. The capital letter in the brackets indicate the wear stages according to Weers, (1990) and Weers and Montoya (1996). L: length; W: width; EH: enamel height on the lingual side; EH/L: ratio between the enamel height and the length of the tooth; Hs: distance between the hypoflexus (sinus) and the crown-base on the lingual side (see text for details); x̄: mean value; PRP: Perpignan (=Serrat d'en Vaquer); BRS: Brisighella; VRD: Verduno; PIK: Pikermi; KMK: Kemiklitepe; GAN: Guansu; LUF: Lufeng; MLY: Molayan; IVN: Ivand 1; PER: Perrier; PN: Pirro Nord. Data of *H. depereti* are from are from Masini & Rook (1993), Sen (2001b), Weers & Rook (2003); Weers (2004) and this work; data of *H. primigenia* are from Weers & Rook (2003); data of *H. gansuensis* are from Wang & Qiu (2001); data of *H. lufengensis* are from and Weers (2004) and Wang & Qi (2005); data of *H. aryanensis* are from Sen (2001b); Sen & Purabrishemi (2010); data of *H. refossa* from Perrier are from Weers (1994); data of *H. refossa* from Pirro Nord are from Rook & Sardella (2013) with addings. All measures are in mm.

Species	BP	LP	GL	SD
H. depereti (MGPT-PU 128349)	~18,45	10,97	/	8,20
H. refossa (MGPT-PU 124726)	20,21	12,35	/	?
H. refossa (MGPT-PU 105170)	18,55	10,73	82,11	8,17
H. cristata (no number)	11,55	6,34	66,12	6,52

Tab. 2 - Measurements of radial bones of some specimens of Neogene and extant species of *Hystrix* from Italy: *H. depereti* from Moncucco Torinese, Piedmont, Italy (late Messinian, late Turolian, MN 13), *H. refossa* from Pirro Nord, Apulia, Italy (Early Pleistocene, early Biharian); *H. cristata*, recent from Italy. BP: breadth of the proximal head; LP; Length of the proximal head; GL: greatest length of the radius; SD: smallest breadth of diaphysis. All measures are in mm.

strix of Eurasia. The dental remains of *H. lufengensis* differ from the specimen from Verduno for a much lower degree of hypsodonty (see data in Weers (2004) and Wang & Qi (2005)) and for a very low Hs. *H. caucasica* differs from the material from Verduno for its large size and low degree of hypsodonty (Lopatin et al. 2003; Weers 2004), *H. trofimovi* exhibits low crowned teeth that clearly indicate a different taxonomic allocation compared to the single tooth from Verduno. *H. zhengi* (Weers & Zhaoqun 1999; Wang & Qiu 2002; Weers & Rook 2003) a Late Pliocene porcupine from China is exclusively known for several p4. The size of this species is smaller than that of *H. depereti* and similar to that of *H. primigenia*.

Compared to the Miocene and Early Pliocene European species, the single tooth from Verduno exhibits a higher degree of hypsodonty than *Hystrix primigenia* from Late Miocene localities of Eastern and South-Eastern Europe (Weers & Rook 2003). The EH/L index of *H. primigenia* usually is below 100, whereas the mean values known for *H. depereti* are higher than 100 (Weers & Rook 2003). The Hs value has never been formally calculated for *H. primigenia*. However, Sen (2001a) reported a distance of 7-8 mm for the sample of M1-2 from Pikermi, the type locality of this species. These values are clearly lower than those observed for the specimen from Verduno (Tab.1). With respect to *Hystrix depereti*, the size and hypsodonty of the single M1/2 from Verduno are perfectly consistent with the range observed in this species (Sen 2001a; Weers & Rook 2003). The Hs has never been evaluated for the M1/2 from the type locality of Serrat d'en Vaquer. However, Sen (2001a) reported that "on two moderately worn M1 or M2 from Perpignan [= Serrat d'en

Vaquer], the hypoflexus is lost although the crown height measures over 10 mm". This indicates that the Hs in *H. depereti* is higher than in *H. primigenia* and it is consistent with the value of 12.2 mm observed in the tooth from Verduno. Finally, the size and hypsodonty are extremely similar to those reported for the specimens found in the coeval Italian locality of Brisighella (Weers & Rook 2003). Porcupine remains from Brisighella were formerly referred to as *Hystrix primigenia* by Masini & Rook (1993) and subsequently assigned to *Hystrix depereti* by Weers & Rook (2003) based on the high degree of hypsodonty of the teeth.

The single tooth from Verduno has been directly compared with several isolated M1/2 belonging to *Hystrix refossa* from the Early Pleistocene of Pirro Nord (Pavia et al. 2012). The teeth of this species differ from that of Verduno in having a less squared profile of the occlusal surface and a slightly less complex occlusal pattern with shallower flexi/ids resulting in less pronounced and less developed enamel islets in worn teeth (Sen 1999). Moreover, as testified by the material from the type locality (fig. 2B in Sen 2001a), *H. depereti* can display well-developed mesostyles in upper cheek teeth that are absent or much less pronounced in *H. refossa*, whereas the presence of a deep mesostyle is clearly evident in the worn specimen from Verduno. The main distinctive characteristic is the higher degree of hypsodonty of *H. refossa* revealed by the higher values of the EH/L index and Hs (Tab. 1).

Finally, the remarkable large size of the studied specimen and the lower EH/L index clearly exclude any possible attribution to the Pleistocene-Holocene Eurasian species of the subgenus *Acanthion*: *Hystrix (A.) vinogradovi*, *H. (A.) lagrelli* and *H. (A.) brachyura* (Weers 1995, 2003a, 2003b; Baryshnikov 2003).

In summary, the single tooth from Verduno can be assigned to the large-sized and semi-hypsodont (sensu Sen & Purabrishemi 2010; Nishioka et al. 2011) porcupine *Hystrix (H.) depereti*

Radius. The above described incomplete radius has been compared with two radii of the Pleistocene species *Hystrix refossa* from Pirro Nord (Apulia, Southern Italy) belonging to different adult individuals and one sub-adult of the extant crested porcupine *H. cristata* from Italy (Tab. 2). The morphology of the radius from Moncucco Torinese is consistent with those of *H. refossa* and *H. cristata* for the general structure and only very small differences might be recognized between these three taxa. The overall size of the radius from Moncucco Torinese is comparable to that of *H. refossa* from Pirro Nord, whereas that of *H. cristata* is evidently much smaller. The surface for the attachment of the *membrana interossea antebrachii* is well developed in all the examined species. However, in the radius from Moncucco Torinese it is wider, deeper and much

more defined, while it appears slightly narrower and more elongated in *H. refossa*. Moreover, the specimen from Moncucco Torinese exhibits a slightly less expanded lateral region of the radial head compared to *H. refossa* and *H. cristata*. The radius from Moncucco Torinese can be unquestionably assigned to a large sized porcupine species of the genus *Hystrix*.

Remarks. During the late Miocene, two large sized porcupine species were present in Europe, *H. depereti* and *H. primigenia*. The former was widespread in South-Western Europe (Spain, Italy and France) (Sen & Purabrishemi 2010) whereas the latter occurred in South-Eastern Europe and Western Asia (Greece, Macedonian Republic, Moldavia, Bulgaria and Turkey) (Sen & Purabrishemi 2010). In particular, during the latest Messinian, between 5.55 and 5.33 Ma, *Hystrix depereti* was present at Brisighella, Central Italy, but also in NW Italy, as demonstrated by the herein described single tooth recovered at Verduno. The osteological differences between the postcranial elements of these two species are still not properly defined and, more generally, the morphology of the radial bone of the Old World porcupines seems to be rather conservative. However, because of the well-documented presence of the species *H. depereti* in NW and Central Italy during the uppermost interval of the Messinian stage, the partially complete radius from Moncucco Torinese described herein is referred to *Hystrix (H.) depereti*.

Discussion

Morphofunctional remarks

Despite being only partially complete, the preserved portion of the radius allows to set out several morphofunctional considerations. The head of the radius exhibits an elongated ovoid shape with a quite convex ventral surface where it was connected with the radial notch of the ulna. The rounded shape of the ulnar facet likely allowed a certain degree of mobility at the radio-ulnar joint, thereby assisting the rotation of the radius during supination-pronation movements of the ante-brachium. However, as in all extant Old World porcupines, supination-pronation ability was less extensive than in other hystricognath rodents such as the extant Erethizonthidae, the New World porcupines that are characterized by arboreal habits (Candela & Picasso 2008). The more circular head of the radius, as in the case of New World porcupines, further facilitates the pronation-supination movements of the antebrachium and is quite common in arboreal species (MacLeod & Rose 1993). Conversely, a more rectangular shape, and a flattened and less developed ulnar facet limits the rotation of the radius stabilizing the elbow junction and is more typical in specialized cursorial taxa as for example

the hystricognath rodent *Dolicothis* (Macleod & Rose 1993; Candela & Picasso 2008). Intermediate conditions are usually found in fossorial and generalized terrestrial taxa. From the ecological point of view, the extant Old World porcupines are considered terrestrial and/or semifossorial (Santini 1980; Nowak & Paradiso 1983; Weisbecker & Schmid 2007; Samuels & van Valkenburgh 2008). They can cover remarkably long distances while foraging (Santini 1980; Nowak & Paradiso 1983) and are also able to dig subterranean extended and quite complex dens that require some burrowing ability (Nowak & Paradiso 1983; Weisbecker & Schmid 2007). Moreover, they are also known to be good swimmers (Nowak & Paradiso 1983). The observed morphology of the radius documented in this paper is consistent with such a generalized mobility behavior. Indeed, a certain degree of pronation-supination movements of the ante-brachium is possible due to the convexity and the quite expanded ulnar facet. Pronation and supination are useful in feeding habits for manipulating food as can be observed in extant *Hystrix* species. Moreover, pronation is also useful in providing force during excavation (Elissamburu & De Santis 2011). However, in the studied radius from Moncucco Torinese, these morphological features do not seem to affect the stability during parasagittal movements of the ante-brachium since the humeral-radial contact of the elbow was rather stable due to the quite elongated radial head and the rather well developed capitular eminence (Candela & Picasso 2008). Finally, the radius from Moncucco Torinese displays a stout structure with a robust neck and a quite broad proximal end of the bone shaft displaying an enlarged medial margin and a prominent marginal crest. As previously observed in many groups of rodents including the genus *Hystrix*, these regions of the bone are devoted to the attachment of the muscles of the forearm, in particular the *supinator brevis* and *flexor digitorum profundus* muscles (Parssons 1894; Holliger 1916; Hill 1937; Thorington et al. 1997) that were probably strongly developed in *H. depereti.* Strong flexor, pronator and supinator musculatures are usually related to digging rather than to locomotion in rodents (Elissamburu & De Santis 2011), thus being consistent with burrowing habits (Wood 1962). However further analyses and more complete material are necessary to conclusively evaluate the digging hability in *H. depereti.*

In conclusion, the general structure of the radius from Moncucco Torinese described herein evidences a remarkable correspondence with extant *Hystrix* and suggests that the larger Miocene species *Hystrix depereti* displayed a generalized terrestrial behavior, even if some burrowing abilities cannot be excluded. Additional analyses on post-cranial remains are necessary in order to clearly define the locomotory behaviour and the ecological features of Neogene giant forms of *Hystrix* in order to properly interpret the possible differences with extant Old World porcupines.

Paleoecology

Currently, the subgenus *Hystrix* occurs exclusively in temperate and warm biotopes and its presence as fossil is generally regarded as indicative of tropical to warm temperate climatic conditions (Tong 2008). They are currently found in a variety of environments such as shrublands, maquis, steppes, forests and even dry rocky areas. However, these rodents prefer areas with adequate vegetation cover (Santini 1980). They can burrow their own dens but they can also find diurnal repair under rock crevices or in abandoned dens. The ecological requirements of *Hystrix* are quite complex and depend on their nocturnal feeding habits. Extant porcupines of the subgenus *Hystrix* need at least a minimum of 7 h night duration that exclude latitudes higher than 44°-46° (Alkon & Saltz 1988; Mori et al. 2013). Moreover, average annual temperature lower than 10°C seems to be a further limiting ecological factor (Tong 2008). These data probably concur to explain the absence in Italy of large porcupines of the subgenus *Hystrix* after the late Early Pleistocene climate transition (Berger et al. 1993). Conversely, the smaller *Hystrix (Acanthion) vinogradovi* is sometimes recorded even in the Middle and Late Pleistocene (Iurino et al. 2015; Kotsakis et al. 2003; Salari & Sardella 2009). However, this small-sized species is closely related to the extant Himalayan porcupine *Hystrix (Acanthion) brachyura* that can tolerate lower temperatures (Mori et al. 2013). *H. (A.) vinogradovi* was less termophilous than other porcupines (Baryshnikov 2003) and has been also found at high latitudes and/or altitudes (Salari & Sardella 2009; Vekua et al. 2010). The occurrence of a large-sized porcupine of the subgenus *Hystrix* in the latest Messinian of NW Italy suggests the existence of a subtropical to warm temperate climatic regime for that area or, in any case, the absence of severely cold climatic conditions.

Palaeobiogeographical notes

According to the revision of Weers and Rook (2003), *H. depereti* is considered a large-sized species occurring in most of Europe including the Iberian Peninsula, Italian Peninsula, Balkans and central Europe between Late Miocene and Early Pliocene (Turolian and Ruscinian, MN 12-15), whereas the more brachyodont species *H. primigenia* occurred in Western and Southern Asia and Southeast Europe during the Late Miocene (Turolian, MN 11-13). These conclusions were only partially accepted by Sen & Purabrishemi (2010) that suggested that *Hystrix depereti* was widespread only in Southwestern Europe in the latest Miocene-Early

Pliocene (late Turolian and Ruscinian, MN13-MN15) whereas *H. primigenia* was present in the Balkans and western Asia in the late Miocene (middle-late Turolian, MN12-MN 13). Moreover, some other authors (Lopatin et al. 2003; Kovachev 2012) did not accept this revision and maintained the name of *H. depereti* only for the porcupine remains from the type locality of Serrat d'en Vaquer (Early Pliocene, Ruscinian, MN 15). However, our results indicate that *H. depereti* was a common taxon of Southwestern Europe at the end of the Miocene and in the Early Pliocene. In particular, this species occurs in the coeval locality of Brisighella where most of the rodent taxa of Verduno are also present (De Giuli 1989; Colombero et al. 2013, 2014a), thereby providing evidence of the high similarity between these two localities.

Conclusions

The hystricid material from Moncucco Torinese and Verduno described herein improves our knowledge about the latest Messinian rodent communities of NW Italy. From the biochronological point of view, the occurrence of *Hystrix depereti* is consistent with the other rodent taxa found in these localities. This species appeared during the Messinian in Western Europe (Teruel, Las Casiones; see Weers & Rook 2003). Slightly before the Mio/Pliocene boundary, it was present also in Italy thus testifying the strong connection of the Italian peninsula with the western regions of Europe towards the end of the Messinian Salinity Crisis. This strong relationship is further testified by the occurrence in the latest Messinian of Italy of the rodent genera *Apocricetus* and *Stephanomys* for which the Italian Peninsula represents the easternmost record (De Giuli 1989; Colombero et al. 2013). The stratigraphic record of *Hystrix depereti* supports the hypothesis that the Turolian/Ruscinian mammal renewal was not an abrupt event but that the biochronological range of some Turolian rodent taxa could also extend in the Ruscinian. Moreover, as testified by the rodent assemblage of Moncucco Torinese and Verduno (Colombero et al. 2013, 2014a; Mansino et al. 2014), taxa that were rather common during the Early Pliocene such as *Sciurus warthae*, *Apocricetus barrierei*, *Neocricetodon magnus* and *Occitanomys brailloni* were already present during the latest Messinian in the eastern and central sectors of the Mediterranean basin.

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