

Late Neogene and Quaternary lagomorphs from Tuscany: a revision based on specimens in Basel Naturhistorisches Museum and Florence University collections

Chiara Angelone · Lorenzo Rook

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Abstract A revision of the Late Turolian (Messinian)–Biharian (Early Pleistocene) lagomorphs from Tuscany kept in the collections of the Basel Naturhistorisches Museum is the basis for increasing our knowledge on the Late Neogene and Quaternary Italian lagomorph record. The study of the NMB collection has been combined with a revision of coeval Tuscan lagomorphs recorded in the collections of the University of Florence. The taxa herein studied and described represent three leporids (*Alilepus meini* from the Early Messinian of Baccinello V3, *Trischizolagus* sp. from the latest Messinian of Borro Strolla, and *Oryctolagus valdarnensis* from the Early Pleistocene of Upper Valdarno) and two ochotonids (*Prolagus* cf. *sorbini* from the Early Messinian of Velona and the latest Messinian to earliest Pliocene of Borro Strolla, and *Prolagus* aff. *sorbini* from the Late Pliocene of Arcille and the Early Pleistocene of Upper Valdarno). The taxonomic study is completed with notes on evolutionary tendencies and palaeobiogeography of the studied species.

Keywords Lagomorpha · Taxonomy · Evolutionary/phylogenetic tendencies · Palaeobiogeography · Peninsular Italy · Late Neogene · Early Pleistocene

Abbreviations

FU	Faunal Unit
NMB	Basel Naturhistorisches Museums
IGF	“Museo di Storia Naturale” (Geology and Palaeontology Section) of the University of Florence
<i>L</i>	Length
<i>W</i>	Width
PH	Hypoflexus depth
AA	Partial width (sensu Angelone and Sesé 2009)
Ltrig	Trigonid length
Ltal	Talonid length
Wtrig	Trigonid width
Wtal	Talonid width

Introduction

This paper offers a synthetic overview of the lagomorph record in the Late Neogene and Quaternary of Tuscany. This paper was conceived after the revision of material kept in the collections of the Basel Naturhistorisches Museum. Given Burkart Engesser’s recognized outstanding expertise in rodents, at first glance the reader could be surprised to find a paper dealing with lagomorphs in the frame of this volume. As a matter of fact, as field paleontologist, an important contribution of Burkart Engesser is the survey and documentation of the Late Miocene mammal-bearing localities of the Baccinello Basin in southern Tuscany (Hürzeler and Engesser 1976; Engesser 1983, 1989, 2000; Rook et al. 1996, 1999). His interest in fossiliferous localities in Italy is grounded not only on the steps of his professor, the late Prof. Johannes Hürzeler (1908–1995), but is actually framed into a long-lasting

C. Angelone
Dipartimento di Scienze Geologiche, Università Roma Tre,
Largo San Leonardo Murialdo 1, 00146 Rome, Italy
e-mail: angelone@uniroma3.it

L. Rook (✉)
Dipartimento di Scienze della Terra, Università di Firenze,
Via La Pira 4, 50121 Florence, Italy
e-mail: lorenzo.rook@unifi.it

interest of Basel palaeontologists on the vertebrate fossil record of Tuscany.

On the occasion of a recent visit to the NMB, we had opportunity to study the Late Neogene and Quaternary record of Italian lagomorphs in the Basel collections and we found out that the Italian record of lagomorph was in deep need of a revision. A detailed study of such material has never been accomplished and the available descriptions are not adequate to present-day understanding of the evolutionary history of these taxa. The same was true for part of the lagomorph fossil record in the collections of the Florence University. Thus we are taking this opportunity for preparing a comprehensive review. All the studied material comes from fossiliferous localities of Tuscany, Italy (Fig. 1). The studied taxa are:

- two species of the ochotonid *Prolagus*. One species from the Early Messinian of Velona and the latest Messinian to earliest Pliocene of Borro Strolla; the other from the Late Pliocene (Early Villányian; MN16a) of Arcille and from the Early Pleistocene (latest Villányian–earliest Biharian) of Upper Valdarno (Olivola and Tasso Faunal Units);
- the latest Miocene leporid *Alilepus* from Baccinello V3 (MN 13);
- the leporid *Trischizolagus* from the latest Messinian of Borro Strolla;
- the leporid *Oryctolagus* from the Early Pleistocene (Early Biharian) of Upper Valdarno (Tasso Faunal Unit).

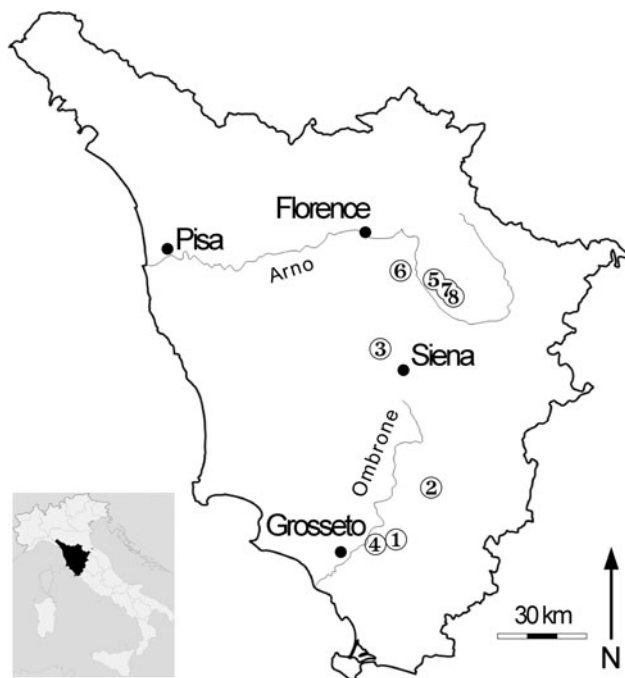


Fig. 1 Location map of studied lagomorph-bearing localities from Tuscany recorded in the NMB and the IGF. 1 Baccinello V3, 2 Velona, 3 Borro Strolla, 4 Arcille, 5–8 Upper Valdarno (5 Solava, 6 Castello Incisa, 7 Case Inferno, 8 Strette al Tasso)

Also available for study was the Late Miocene insular endemic ochotonid *Paludotona* from Baccinello (V0–V2). However, *Paludotona*, due to its unresolved phylogenetic origins and the temporal and palaeobiogeographical problems related to its arrival on the Tusco-Sardinian palaeobioprovince, deserves to be the subject of a separate paper.

Materials and methods

The studied material consists of upper and lower jaws and isolated teeth. It is housed in the Basel Naturhistorisches Museums and in the Natural History Museum (Geology and Palaeontology Section) of the University of Florence. The list of additional material from other institutions assigned to the species here reviewed is reported in [Appendix 1](#).

The occlusal surface of each tooth was drawn using a camera lucida mounted on a Leica MS5 binocular microscope. SEM images were performed for unworn, problematic or very damaged individuals. Occlusal measurements were taken from the drawings. The measurements introduced for ochotonids by Angelone and Sesé (2009) are here used also for leporid teeth (see Angelone and Rook 2011). The nomenclature (Fig. 2) follows Angelone and Sesé (2009) for ochotonids and López Martínez et al. (2007) integrated with Palacios and López Martínez (1980) for leporids.

For biochronological references we follow Sala and Masini (2007) and Rook and Martínez-Navarro (2010). Although still contested within the Quaternarist community (cfr. Van Couvering et al. 2009; McGowran et al. 2009), we follow here the recent formal IUGS recognition (June 2009) of Quaternary as a Period/System with the re-designation of the base of the Pleistocene Series/Epoch in the 2.59 Ma GSSP of the Gelasian Stage.

Fossil localities: geological setting and age attribution

Latest Turolian (latest Miocene)

Baccinello V3

The geology and palaeontology of the Baccinello area (Grosseto district) are well known thanks to the early research led by J. Hürzeler (1908–1995) from the NMB (De Terra 1956; Gillet et al. 1965; Lorenz 1968), which recovered abundant faunal remains from well-documented stratigraphic levels (Hürzeler and Engesser 1976).

The Baccinello Basin records a continental sedimentation throughout the late Tortonian–Messinian. Fossiliferous deposits in the different units recognized within the Basin

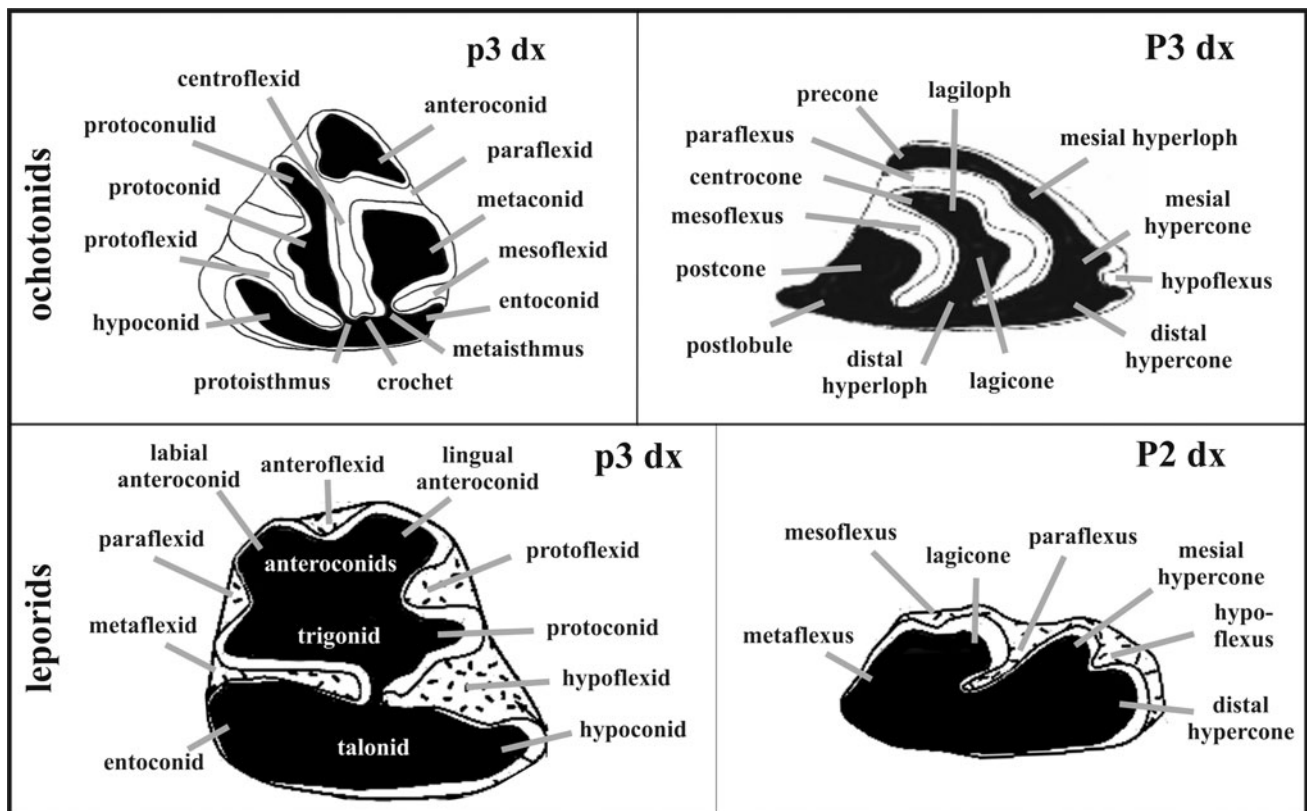


Fig. 2 Nomenclatorial synopsis. Ochotonids from Angelone and Sesé (2009); leporids from Palacios and López Martínez (1980) integrated with López Martínez et al. (2007)

(Lorenz 1968; Benvenuti et al. 2001) bear relatively abundant fossil mammal remains that are grouped into distinct assemblages (vertebrate assemblages V0, V1, V2, and V3; Lorenz 1968; Rook et al. 1996, 1999, 2000). Early Pliocene marine deposits, ascribed to the *Sphaeroidinellopsis* Zone, unconformably overlie the Late Miocene sedimentary succession (Bossio et al. 1991; Benvenuti et al. 2001). Rook et al. (2011) provided a synthesis of the Baccinello geological setting, and support the chronological range of the depositional history of the sedimentary succession based on a well-resolved magnetostratigraphic study, where the Baccinello V3 fauna is correlated to Chron C3An, Early Messinian, ca. 6.733–6.436 Ma (Mammal zone MN13). Leporid remains (since Hürzeler and Engesser 1976 on, see synonymic list) and a *Prolagus* (B. Engesser pers. com. in Rook and Masini 1990) were reported from Baccinello V3 but never described.

Velona Basin

The Velona Basin is located in southern Tuscany, about 40 km south of Siena. It is a small Basin (approx. 5 km long and 4 km wide), characterized by a 250-m-thick

succession, dominated by continental terrigenous sediments, and made up by two main synthems separated by an angular unconformity (Rook and Ghetti 1997; Ghetti et al. 2002). The lower synthem can be subdivided into six concordant fluvio-lacustrine subunits, interpreted as Early Messinian ('pre-evaporitic') in age (Rook and Ghetti 1997; Ghetti et al. 2002). The upper synthem has a very limited extension and is composed only by alluvial conglomerates, interpreted as the last stage of deposition of the Basin. No element exists to determine the age of these coarse deposits and they may be referred to the top of the Messinian or, at least, to the very Early Pliocene (Martini and Sagri 1993; Ghetti et al. 2002).

The small mammal fauna recovered from the fluvio-lacustrine subunit of the lower synthem of this Basin (Rook and Ghetti 1997; Ghetti et al. 2002) refers to the Late Miocene, bearing no evidence of the endemic Late Miocene "*Oreopithecus*" faunas (OZF in Bernor et al. 2001) common in other nearby basins in southern Tuscany (cfr. the Baccinello–Cinigiano Basin). This fact leads to consider the beginning of sedimentation in the Velona Basin to be more recent than in other contiguous basins (Rook and Ghetti 1997; Ghetti et al. 2002).

Borro Strolla

The Borro Strolla area is located in the southeastern end of the Valdelsa Basin. The latter is a 25 km wide and 60 km long, located about 45 km SE of Florence, and is filled with more than 2,000 m of Neogene and Quaternary sediments. From a stratigraphic point of view the Neogene sediments exposed in the Valdelsa Basin, mostly of Pliocene age, have been included in a stratigraphic framework based on unconformity-bounded units (Benvenuti and Degli Innocenti 2001). In the Borro Strolla valley a succession including the Miocene–Pliocene transition has been described by Bossio et al. (2001) and, according to the recent revisions by Benvenuti and Degli Innocenti (2001) and Abbazzi et al. (2008), sediment outcroppings in the area of Borro Strolla may represent part of the oldest basin infill (Borro Strolla synthem) within the Valdelsa Basin latest Miocene–Pliocene succession. Late Miocene sediments, unconformably overlain by the Pliocene succession, crop out to a limited extent in other nearby Valdelsa Basin area, and are widely exposed in the so-called Casino Basin (Lazarotto and Sandrelli 1977; Bossio et al. 2001; Rook et al. 2008). The field recognition of unconformities or inferences on unconformable transitions supported by facies relations and biochronologic considerations allowed Abbazzi et al. (2008) to subdivide uppermost Messinian–earliest Zanclean deposits into three unconformity-bounded units consisting of various lithofacies associations indicative of different palaeoenvironments developed in this area at the Mio-Pliocene transition.

A small sample of fossil mammals has been recovered at Borro Strolla from sub-synthem BS-1 (chronologically interpreted as latest Messinian in age), while only one specimen of *Prolagus* has been recovered from the following sub-synthem BS-2 (interpreted as representing the Messinian–Zanclean transition) (Abbazzi et al. 2008). From sub-synthem BS-1, at least 12 taxa are documented. The large mammal assemblage includes two bovids (the mid-sized spiral-horned *Samotragus* sp., and a larger bovid determined as *Palaeoryx–Protoryx* group), a large-sized giraffid, and the cervid *Paracervulus*. Small mammals include the insectivore *Galerix* aff. *depereti*, six rodents (*Apocricetus barrierei*, *Apodemus* cf. *gudrunae*, *Stephanomys* aff. *donnezani*, *Centralomys benedicetti*, *Debruijnmys* sp. and Sciuridae indet.), the ochotonid *Prolagus* and a leporid (Abbazzi et al. 2008). The Borro Strolla mammal assemblage suggests palaeobiogeographic connections with western Europe, fitting the general aspect of a fauna at the Mio-Pliocene boundary. The co-occurrence of terrestrial molluscs from the same sediments with a Pliocene affinity, offers further biochronologic constraints supporting the calibration of the Borro Strolla fluvial deposits to the latest Messinian–earliest Zanclean.

Early Villányian (Late Pliocene)

Arcille

“Fosso di Puntolungo” (known in literature as Arcille, from the name of the nearby hamlet) is the youngest fossiliferous locality in the area of the Baccinello Basin (Grosseto district). The fossiliferous sediments are levels of lignitic shale interbedded within the Pliocene marine deposits that unconformably overlie the Late Miocene continental deposits of the Baccinello V0–V3 sedimentary succession. Arcille yielded a small mammal assemblage first reported by Hürzeler and Engesser (1976) on the basis of material excavated by J. Hürzeler in 1954 during one of his first surveys in the Baccinello area. The small mammal assemblage includes the vole *Mimomys hassiacus* (Masini and Torre 1987) and can be referred to the *Mimomys hajnackensis* zone of the Early Villányian.

Arcille represents one of the few known Early Villányian assemblages of Italy (Sala and Masini 2007), together with the rich faunal assemblages of Cascina Arondelli in the area of Villafranca d’Asti in Piedmont (Berzi et al. 1967; Fejfar 2001) and San Giusto from the Lower Valdarno in Tuscany (the type locality for *Mimomys stehlini*; Forsyth Major 1902; Masini and Torre 1987). These faunas are coeval with the Early Villafranchian large mammal assemblages of the Triversa Faunal Unit (Maul et al. 1998; Rook and Martínez-Navarro 2010) and correlated to the Gauss Magnetochron, below the top of the Kaena event (C2An.2–C2An.1) with an inferred geochronometric age of 3.60–3.10 Ma (Napoleone et al. 2003). Hürzeler and Engesser (1976) mentioned the occurrence of *Prolagus* in the Arcille faunal list, but a description of the material was never provided.

Late Villányian/Early Biharian (Early Pleistocene)

Upper Valdarno Basin

The lagomorph record from Upper Valdarno is known since early papers (Falconer 1865, 1868; Bosco 1899a, b). The revision of this material faces the problem that often occurs when revising material from historical collection. In most cases in fact, there is no indication of the exact provenance of the specimens and the labels just reports “Upper Valdarno”. When the topographic indication is given, in most cases it is possible to establish, at least with some approximation, the general stratigraphic unit of provenance.

The Upper Valdarno record is celebrated for the well-known large mammal collections, whereas the small mammals have a documentation that is not even comparable with that of large mammals (Cioppi and Dominici

2011; Rook et al. 2012). Despite the scanty record of small mammals the lower portion of the second sedimentary phase of the Basin infilling (the Montevarchi synthem) yielded a few vole remains that allowed to identify the *Mimomys polonicus* zone (Late Villányian, earliest Pleistocene) in sediments characterized by reversed magnetization, referred to the pre-Reunion interval of the Matuyama Chron (Napoleone et al. 2003; Ghinassi et al. 2004, 2005).

In the upper part of the same sedimentary complex (the Montevarchi synthem) is located the Castelfranco di Sopra site. The latter is the type locality of *Mimomys pliocaenicus*, the vole that defines the homonymous zone of the Late Villányian (Early Pleistocene; Masini and Torre 1987). Several local faunas bearing large mammals, grouped in the Olivola FU, are indirectly referred to the *M. pliocaenicus* zone (Torre et al. 1996, 2001). The sediment outcroppings in these localities are directly correlated with the interval between Reunion and early part of Olduvai Subchrons (Napoleone et al. 2003).

The uppermost portion of the sedimentary complex belonging to the Montevarchi synthem yielded abundant large mammals typical of the Tasso FU. The transition from the Olivola FU to the subsequent Tasso FU (within the Late Villafranchian) is accomplished mainly by dispersal events (Torre et al. 1992, 2001), which succeeded in a time span that has been magnetostratigraphically calibrated close to the top of the Olduvai Subchron (Napoleone et al. 2003). It thus corresponds to the mid part of Early Pleistocene (or the former Pliocene–Pleistocene boundary) at the Gelasian/Calabrian boundary as defined at the La Vrica section (Aguirre and Pasini 1985; Albianelli et al. 2002). The transition between Olivola and Tasso FUs is thus placed within an interval of gradual climatic transition, which mirrors the gradual change in large mammals faunal composition (Rook and Martínez-Navarro 2010). Few remains of *Mimomys savini* came from these Upper Valdarno localities: Case Inferno and Le Strette (Torre 1985), that allow recognizing the occurrence of Early Biharian small mammal assemblage within the Tasso FU (Sala and Masini 2007).

Rook and Masini (1990) reported the occurrence of the ochotonid *Prolagus* both in the Late Villányian (a fragmentary mandible from Solava) and in the Early Biharian (a fragmentary mandible from Case Inferno). The site of Solava is located near Figline Valdarno and is correlatable with the site of Poggio Rosso, Olivola FU (Napoleone et al., 2001), whereas Case Inferno (in literature also referred to as “Inferno”, or “L’Inferno”), one of the most celebrated sites of the Tasso FU, yielded *Mimomys savini* remains and it is thus correlatable to the Early Biharian.

Systematic palaeontology

Order Lagomorpha Brandt, 1855
 Family Ochotonidae Thomas, 1897
 Genus *Prolagus* Pomel, 1852
Prolagus cf. *sorbini* Masini, 1989
 Figure 3a–l, measures in Table 1

1997 *Prolagus* ex gr. *sorbini-michauxi* Rook and Ghetti, p. 341, 343; p. 344, fig. 4a–d.

2002 *Prolagus* ex gr. *sorbini-michauxi* Ghetti et al., p. 8, tab. 2; p. 16.

2007 *Prolagus* cf. *P. sorbini* Angelone, p. 411, fig. 4a–d; p. 412, tab. 1; p. 414 text and fig. 6; p. 418; p. 419.

2008 *Prolagus sorbini* Abbazzi et al., p. 620, tab. 1; p. 621, fig. 6h; p. 621–622.

Localities: Velona Basin and Borro Strolla (Siena).

Age: Messinian to earliest Pliocene.

Material

Velona: P² dx: IGF 9432V; P₃ sin: IGF 9433V; IGF 9434V; IGF 9435V; lower molariform IGF 9476V; M₂ IGF 9477V.

Borro Strolla BS-1: lower jaw sin: IGF 9473V (M₁–M₂ plus a loose P₄); P³ dx: IGF 9451V; P⁴ dx: IGF 9452V; M¹ sin: IGF 9453V; M² sin: IGF 9455V; M² dx: IGF 9470V; D₃ sin: IGF 9456V; P₃ sin: IGF 9454V; P₃ dx: IGF 9469V

Borro Strolla BS-2: upper jaw dx: IGF 9475V (P³–M²)

Description

Upper jaw: premolar foramen lying in front of P⁴. Each teeth position will be described in the corresponding section.

Lower jaw: foramina and other salient features are not visible in this mandible fragment. Talonids are more flattened than trigonids and bear a long isthmus.

P²: (P²: (Fig. 3d) the mesial hyperloph, thin and covering almost all the centrocone is broken in its labial end, but the observation of the shaft of the tooth in its anterior part indicates that the enamel is continuous; para- and mesoflexus are verticalized in their distal end; the mesoflexus is particularly deep, almost reaching the distal edge of the tooth; the postcone is broken, and does not appear large and globous as drawn in Rook and Ghetti (1997) and Angelone (2007); the lagicone is roundish and does not bear an incipient centroloph as pictured in the two cited papers.

P³: (Fig. 3h) quite deep hypoflexus, proximal hypercone much smaller than the distal one; mesial hyperloph

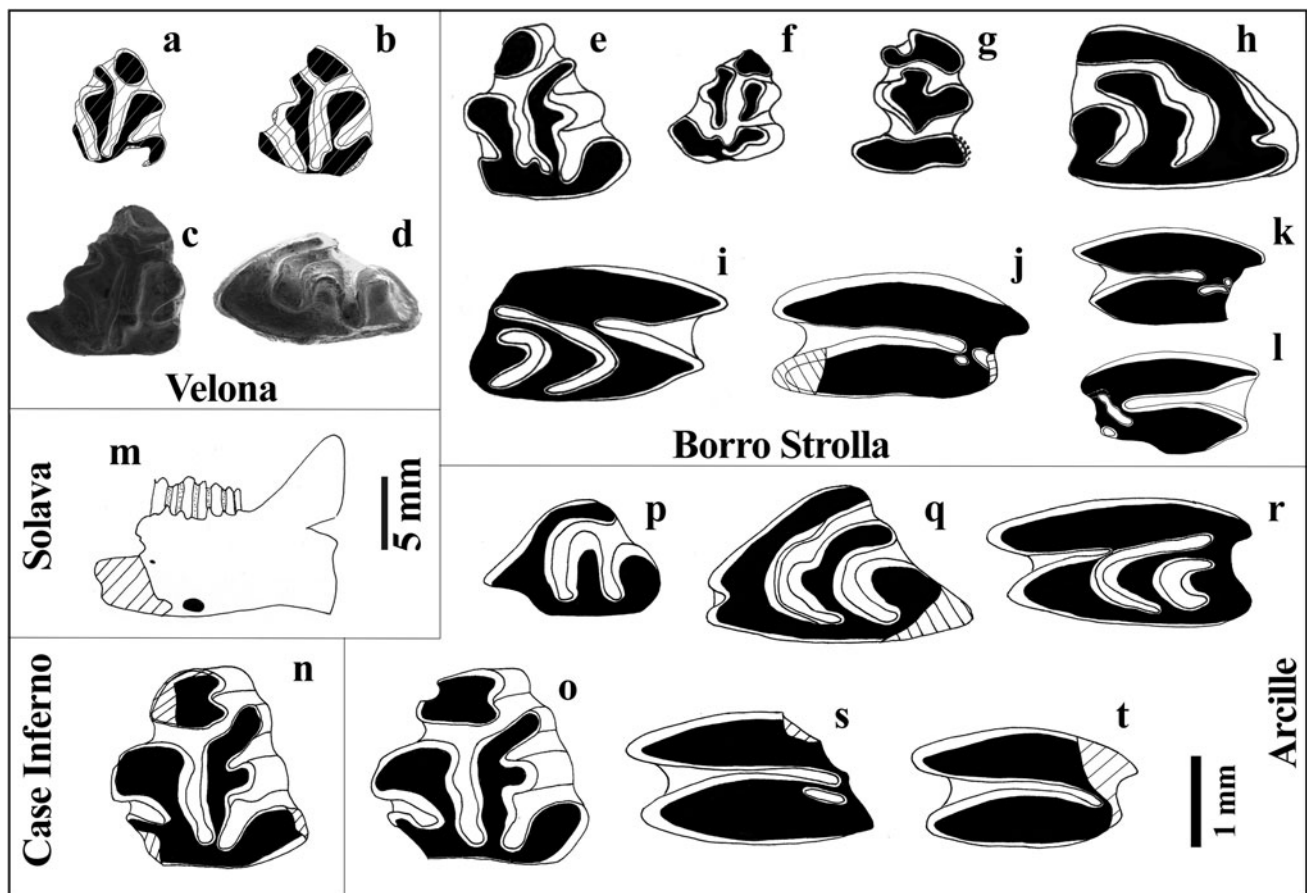


Fig. 3 *Prolagus* cf. *sorbinii*: **a–c**, **f** P₃ sin IGF 9433V, IGF 9434V, IGF 9435V, IGF 9469V; **d** P² dx IGF 9432V; **e** P₃ dx IGF 9454V; **g** D₃ sin IGF 9456V; **h** P³ dx IGF 9451V; **i** P⁴ dx IGF 9452V; **j** M¹ sin

IGF 9453V; **k** M² sin IGF 9455V; **l** M² dx IGF 9470V; *Prolagus* aff. *sorbinii*: **m** lower jaw sin IGF 2827V; **n**, **o** P₃ dx NMB VA2246, NMB FP30; **p–t** P²–M² of upper jaw sin NMB FP29

narrowing in its medial part, with enamel *hiatus*; lagiloph not reaching the outer part of the tooth; the connection between lagicone and lagiloph is sharply indented.

P⁴: (Fig. 3i) proximal hypercone slightly smaller than the distal one; V-shaped hypoflexus not reaching the half of the tooth; parafochette long and curving upwards; C-shaped, long mesofossette.

M¹: (Fig. 3j) hypoflexus deep, very slight undulated, with small, round fossette under its labial end and another oval, slightly larger one positioned after the hypoflexus end. In the “radical” part of the tooth fossettes do not disappear with wear.

M²: (Fig. 3k, l) hypoflexus deep, very slightly undulated in its anterior part in IGF 9455V; one large, bean-like fossette lies under the distal part of its labial end and another smaller, roundish fossette positioned near the labial border at the same height of the hypoflexus; the fossettes do not disappear with wear in IGF 9455V, whereas in IGF 9470V only one fossette is observable in “radical” side; in the less worn individual (IGF 9470V) the parafochette is very elongated labial edge.

D₃: (Fig. 3g) triangular anteroconid, connected to a labial accessory cusp. The metaconid–protoconid complex is characterized by an antero-posterior indentation and it is not connected to the entoconid–hypoconid complex. The entoconid is broken in its anterior lingual part, however, the enamel seems to be continuous around its edge.

P₃: (Fig. 3a–c, e, f) the occlusal surface of two over 3 specimens from Velona (IGF 9433V, IGF 9435V) is very damaged. The tooth is slender ($L > W$); in the specimens from Velona and in the juvenile unworn specimen from Borro Strolla (IGF 9454V) the anteroconid is posteriorly and/or laterally indented, whereas in the more worn specimen from Borro Strolla (IGF 9469V) its outline is smooth. The triangular metaconid is as large or slightly larger than the anteroconid. The mesoflexid is wide, V-shaped, in the specimens from Velona. The entoconid is thick, without enamel hiatus, in most cases as prominent or less prominent than the metaconid; the crochet is developed and displaced towards the metaconid in IGF 9434V (Velona) and IGF 9469V (Borro Strolla), whereas it is extremely reduced/absent in the other two specimens from Velona. In

Table 1 Tooth measurements (in mm) of the lagomorph taxa analyzed in this paper (estimated measurements in parentheses)

<i>Prolagus cf. sorbinii</i>			L	W	AA	PH			
P ²	IGF 9432V	Velona	1.25						
P ³	IGF 9451V	Borro Strolla BS1	1.77		2.33				
P ³	IGF 9475V	Borro Strolla BS2	1.65	2.77	2.13				
P ⁴	IGF 9452V	Borro Strolla BS1	1.44		1.44				
P ⁴	IGF 9475V	Borro Strolla BS2	1.35	3.04	2.65	1.23			
M ¹	IGF 9453V	Borro Strolla BS1	1.37	2.78	2.43	2.14			
M ¹	IGF 9475V	Borro Strolla BS2	1.33	2.92	2.50	2.12			
M ²	IGF 9455V	Borro Strolla BS1	1.06	2.08	2.00	1.44			
M ²	IGF 9470V	Borro Strolla BS1	1.09	(1.87)	1.71	1.46			
M ²	IGF 9475V	Borro Strolla BS2	1.23			2.06			
P ₃	IGF 9434V	Velona	(1.49)						
P ₃	IGF 9435V	Velona	1.74	1.63					
P ₃	IGF 9469V	Borro Strolla BS1	1.84	1.79					
P ₃	IGF 9454V	Borro Strolla BS1	1.18	1.08					
d ₃	IGF 9456V	Borro Strolla BS1	1.54	1.34					
<i>Prolagus aff. sorbinii</i>			L	W	AA	PH			
P ²	NMB FP 29	Arcille	1.24	1.97					
P ³	NMB FP 29	Arcille	1.68		2.05				
P ⁴	NMB FP 29	Arcille	1.35	2.81	2.58	1.34			
M ¹	NMB FP 29	Arcille	1.42	2.56					
M ²	NMB FP 29	Arcille	1.29						
P ₃	IGF 1061V	Arcille	2.52	2.78					
P ₃	NMB FP 30	Arcille	2.16	2.39					
P ₃	NMB VA 2246	Case Inferno	2.22	2.23					
<i>Alilepus meini</i>			L	W	AA	PH	Ltrig	Wtrig	Wtal
P ⁴	NMB BAC 1064	BCB V3	2.12						
M ¹⁽²⁾	NMB BAC 1063	BCB V3	1.97	3.55		2.22			
M [#]	NMB BAC 1061	BCB V3							
P ₄	NMB BAC 1062	BCB V3	2.66				1.36	3.34	2.55
M ₁	NMB BAC 1073	BCB V3						3.00	
<i>Trischizolagus sp.</i>			L	W					
M ²	IGF 9468V	Borro Strolla BS1	1.17						
D ₃	IGF 9464V	Borro Strolla BS1	1.87	1.5					
P ₃	IGF 9467V	Borro Strolla BS1	1.69	1.56					
<i>Oryctolagus valdamensis</i>			L	W					
P ²	IGF 946 (sx)	Castello dell'Incisa	2.40	4.98					
P ²	IGF 946 (dx)	Castello dell'Incisa	2.45	5.02					
P ²	IGF 10130 (sx)	Upper Valdarno	2.45	4.76					
P ²	IGF 10130 (dx)	Upper Valdarno	2.49	4.80					
P ₃	IGF 246V	Case Inferno	(3.33)						
P ₃	IGF 952	Le Strette al Tasso	(2.90)						
P ₃	IGF 10129	Upper Valdarno	4.10	4.07					
P ₃	IGF 12741	Upper Valdarno	4.00	4.10					
P ₃	NMB VA 1798	Tasso	3.19	3.30					
P ₃	NMB VA 2009	Case Inferno	3.40	3.12					

the p3 from Velona the centroflexid is considerably deeper. The metaisthmus is relatively wide, whereas the protoisthmus is thinner. The protoconulid is variable.

In general it can be stated that IGF 9434V from Velona is more similar to IGF 9469V from Borro Strolla than to other P₃ from Velona.

Results

We ascribe *Prolagus* from Borro Strolla to *P. cf. sorbinii* because in spite of showing the main characters that distinguish *P. sorbinii* (e.g.: P₃ with continuous enamel on the thick entoconid; D₃ with accessory labial cusp; P³ with right-angled connection between lagicone and lagiloph, and centrocone not reaching the labial edge of the tooth; P⁴ with relatively short and V-shaped hypoflexus, very long and verticalized parafossette; M¹⁻² with fossettes; Angelone 2007) it shows some peculiar traits. Actually in the specimens from Borro Strolla the overall shape of P₃ is more elongated, the anteroconid is not indented, the entoconid less prominent, the mesoflexus very wide, giving to the metaconid a peculiar triangular shape, the centroflexid is shorter; in D₃ the connection between trigonid and talonid lobe is not present; constant presence in M¹⁻² of two fossettes.

The dimensions of *P. cf. sorbinii* from Borro Strolla are slightly smaller than those of “classic” *P. sorbinii* (Angelone 2007) (Fig. 4a).

Prolagus cf. sorbinii from Velona had already been analyzed in Angelone (2007) and we confirm here its systematic attribution. Its small size and the slender P₃ with triangular metaconid differentiate it from *P. sorbinii* and make it resemble to *P. cf. sorbinii* from Borro Strolla.

We redescribe here *P. cf. sorbinii* from Velona because its morphology was incorrectly drawn in Angelone (2007; cfr. fig. 3a–d and fig. 4a–d, p. 411 in the cited paper). We provide new pictures and references to inventory numbers, lacking in Angelone (2007).

Prolagus aff. sorbinii Masini, 1989.

Figure 3m–t, measures in Table 1.

1935 “...rechtsseitiges Mandibelfragment von *Prolagus*...Basler Naturhistorisches Museums” Tobien, p. 307.

1972 *Prolagus sardus sardus* Fondi, pl. II, fig. 13.

1976 *Prolagus* sp. Hürzeler and Engesser, p. 336.

1990 *Prolagus* gr. *michauxi-calpensis/savagei* Rook and Masini, p. 357, II col., line 16 on; p. 358, fig. 1b; p. 358, tab. 1.

1990 *Prolagus* sp. Rook and Masini, p. 357, II col., line 9 on; p. 358, fig. 1a; p. 358, tab. 1.

1992 *Prolagus* gr. *capensis/savagei* (sic) Sala, p. 212–213.

1994 *Prolagus* sp. Masini et al., p. 382.

1996 *Prolagus* gr. *michauxi-calpensis/savagei* Torre et al., p. 562.

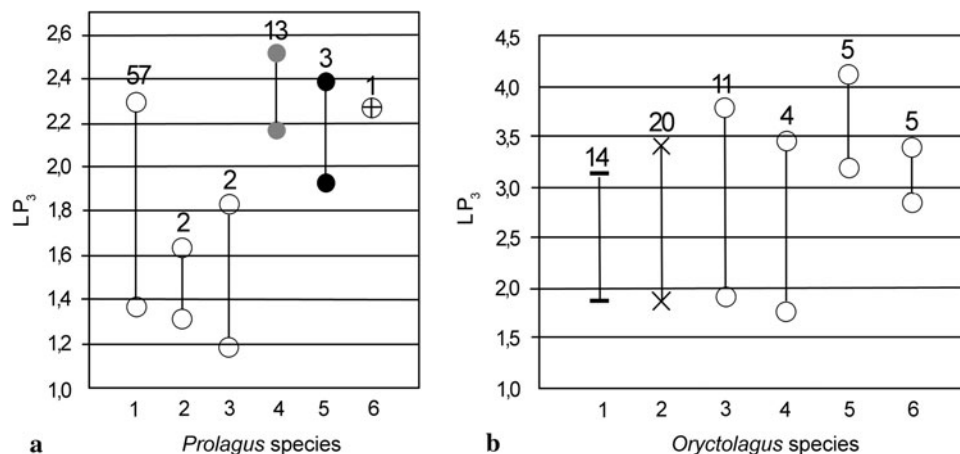


Fig. 4 a Comparisons of P_3 length (LP_3 , in mm) of Italian species of *Prolagus*: 1 *P. sorbinii* (Brisighella 25), 2 *P. cf. sorbinii* (Velona), 3 *P. cf. sorbinii* (Borro Strolla), 4 *P. italicus* (Montagnola Senese + Torre Picchio), 5 *Prolagus* aff. *sorbinii* (Arcille), 6 “*P. savagei*” (Arondelli), (data from Angelone 2007, 2008 and C.A. personal database). **b** Comparisons of LP_3 of Late Pliocene–

Early Pleistocene primitive European species of *Oryctolagus*: 1 *O. laynensis* (Layna, Spain), 2 *O. cf. lacosti* (La Escala, Spain), 3–6 *O. valdarnensis* from Montagnola Senese (3), Torre Picchio (4), Upper Valdarno, Tasso FU (5) and Pirro Nord (6); (data from López Martínez 1989, Angelone 2012, and C.A. personal database). The number on top of size ranges is the number of specimens

2003 *Prolagus* gr. *P. michauxi*-*P. calpensis* Kotsakis et al., p. 319, fig. 5d; p. 338.

Localities: Arcille (Late Pliocene, Grosseto district), Solava (Early Pleistocene, late Villányian, Upper Valdarno Basin) and Case Inferno (Early Pleistocene, Early Biharian, Upper Valdarno Basin).

Age: Late Pliocene–late Early Pleistocene.

Material

Arcille: upper jaw sin: NMB FP29 (broken, only tooth row); lower jaw sin: NMB FP30 (broken, with P_3 – M_1); lower jaw dx: NMB 1601V (broken, with M_1 and loose P_{3-4} and M_2).

Solava: lower jaw sin: IGF 2827V (broken, with P_4 – M_2).

Case Inferno: lower jaw dx: NMB VA2246 (P_3 – M_2).

Description

Lower jaw: (Fig. 3m) on the jaw fragments IGF 1601V and IGF 2827V is still visible a large, round or oval posterior mandibular foramen lying in a very low position (just next to the jaw lower border) and under the anterior part of m_1 . NMB VA2246 is well preserved, but it is mounted on its support with wax, thus the observation of the foramina has not been possible. NMB FP30 is too damaged to provide useful information

P^2 : (Fig. 3p) elongated shape, broken in distal lingual side; long mesial hyperloph with enamel hiatus; elongated lagiloph; equally deep mesoflexus and paraflexus; the paraflexus is slightly widened ant the distal end).

P^3 : (Fig. 3q) mesial hyperloph with enamel hiatus; lagiloph reaching the labial edge of the tooth; connection lagiloph-centrocone marked by a “step”.

P^4 : (Fig. 3r) distal hyperloph longer than mesial one; U-shaped, deep hypoflexus (about 50% of the tooth length); anterior labial part of the parafossette very long and oblique; C-shaped mesofossette.

M^{1-2} : (Fig. 3s, t) very deep, posteriorly curved hypoflexus; in M^1 just posteriorly of the hypoflexus is present a large, elongated, oval fossette.

P_3 : (Fig. 3n, o) triangular, lingually indented anterocoid, as large as metaconid; triangular metaconid, separated from the entoconid in IGF 1601V; deep, U-shaped and posteriorly curved mesoflexid (confluent in the centroflexid in IGF 1601V); thick entoconid, without enamel hiatus; wide metaisthmus (absent in IGF 1601V); protoisthmus variable in width; relatively small protoconid; large protoconulid, especially in NMB FP30 and NMB VA2246; long, undulated centroflexid, curved towards the labial side of the tooth.

Results

Prolagus remains from Arcille and Case Inferno are indeed scanty and separated by about 1.4 Ma. However, their P_3 look very alike. The only difference is that (as should be expected) some characters appear in a slightly more advanced stage in the younger specimen, the one from Case Inferno (e.g., the anteroconid labial indentation is deeper, the protoconid is thinner, the protoconulid is more robust). The lower jaw from Solava lacks its most diagnostic element, the P_3 . However, the fact that it has been found in the Upper Valdarno and the position

of the posterior mandibular foramen similar to the jaw from Arcille, allow us to tentatively assign it to *P. aff. sorbinii*.

The P_3 of *Prolagus* from Arcille and Case Inferno look almost identical to “*P. savagei*” (NW Italy, almost coeval to Arcille; Berzi 1967) and *P. depereti* (Perpignan, Early Pliocene, MN14; López Martínez and Thaler 1975): in all these species we observe $L \approx W$, absence of the crochet, indented anteroconid, oblique centroflexid, developed protoconulid, thick entoconid and similar dimensions. This means that they should all be grouped under “*P. savagei*” that has nomenclatorial priority. However, “*P. savagei*” was reputed an invalid species (López Martínez and Thaler 1975), a decision contested by Azzaroli (1977). Eventually “*P. savagei*” was put in synonymy with *P. calpensis* (López Martínez in Alberdi et al. 1997). In our opinion *P. calpensis* shows characters that are incompatible with the specimens from Tuscany here analyzed and with those of NW Italy (e.g., thin entoconid with enamel hiatus, not indented anteroconid). This nomenclatorial confusion can be settled only after a revision of the mentioned species.

Therefore, as the *Prolagus* remains from Arcille and Case Inferno show some morphological characters in common with the well-characterized species *P. sorbinii* (Messinian–Early Pliocene, MN13–MN14; Angelone 2007), we prefer for the moment to classify them as *Prolagus aff. sorbinii*. This ascription also underlines their possible phylogenetic relationship with *P. sorbinii*. *Prolagus aff. sorbinii* shares with *P. sorbinii*: P_3 with a bent centroflexid, thickened entoconid without enamel hiatus, and indented anteroconid; P^4 with an anteriorly bent, long parafoesette; M^1 retaining one oval foesette (uncommon but observed in *P. sorbinii*). It is also very remarkable the similarity of the post-anteroconid morphology of *Prolagus aff. sorbinii* with juvenile *P. sorbinii*, in which the crochet is absent and the metaconid is often isolated. However, contrarily to *P. sorbinii*, in *P. aff. sorbinii* the P_3 does not bear a crochet, the triangular anteroconid is larger and more flattened, the protoconid is smaller and the protoconulid is thicker; the P^2 has enamel hiatus; the P^4 does not have a V-shaped hypoflexus; there is no foesette on M^2 ; moreover, the P_3 dimensions are quite larger in *P. aff. sorbinii*.

Another species closely related to *P. sorbinii* is *P. italicus* of the Early Pleistocene (MN17) of central Italy (Angelone 2008). The tooth morphology of *P. italicus* is very different from *Prolagus aff. sorbinii*. The most blatant difference is the crenulated enamel band of the former; moreover, the P_3 of *P. italicus* almost always bears a crochet (>90%) in adult individuals, an additional indentation is present in the posterior part of the anteroconid and the centroflexid is straight.

Family Leporidae Fischer De Waldheim, 1817

Genus *Alilepus* Dice, 1931

Alilepus meini Angelone and Rook, 2011

Figure 5a, b; Table 1

1976 Leporidé aff. *Hypolagus* Hürzeler and Engesser, p. 335.

1983 aff. *Hypolagus* sp. De Giuli et al., p. 325.

1986 Leporid aff. *Hypolagus* Azzaroli et al., p. 215.

1989 Leporidae cf. *Hypolagus* sp. Rook 1989, p. 62.

1992 *Alilepus* sp., Rook, p. 142.

1992 cf. *Hypolagus* Rook, p. 142.

1995 *Alilepus* sp. Rook and Torre, p. 380.

1996 *Alilepus* sp. Rook et al., p. 5, Table 1.

1996 Leporidae aff. *Hypolagus* Rook et al., p. 5., tab. 1.

1997 Leporidae aff. *Hypolagus* sp. Kotsakis et al., p. 437.

1997 *Alilepus* sp. Kotsakis et al., p. 437.

1999 *Alilepus* sp. Rook et al., p. 199, tab. 10.3.

1999 aff. *Hypolagus* Rook et al., p. 199, tab. 10.3.

2003 *Alilepus* sp. Fladerer and Fiore, p. 54.

2004 *Alilepus* sp. Rook and Martínez-Navarro, p. 720.

2011 *Alilepus meini* Angelone and Rook, p. 153, fig. 2.

Locality: the material here analyzed has been collected by NMB team from an unrecorded locality referable to level V3 of Baccinello. The type locality of the species is Ribardella (also reported as Ribaldella; cfr. Bernor et al. 2011) and additional material comes from Caprarcce, two of the several fossil-bearing localities of Baccinello V3 in the area of Melacce stream, south of Cinigiano (Angelone and Rook 2011; Bernor et al. 2011).

Age: Early Messinian.

Material: P^4 dx: NMB BAC1064; $M^{1?}$ dx: NMB 1063; upper molariform dx: NMB BAC 1061; P_4 sin: NMB 1062; M_1 dx: NMB BAC 1073.

Description

P^4 : (Fig. 5a) broken in the posterior lingual part, preventing width measurements; distal hyperloph longer than mesial one; hypoflexus very deep (about 75% of W), wide in its central and labial parts, highly crenulated in the mesial part, less crenulated in the distal one.

Upper molariforms: both damaged in the labial posterior part; it is difficult to estimate the lobe proportions and the hypoflexus depth; however, the hypoflexus does not seem as deep as in P^4 and does not widen labially; the hypoflexus is more crenulated in the distal part with respect to the mesial one in $M^{1?}$, whereas it is less crenulated in the mesial than in the distal part in the other upper molariform.

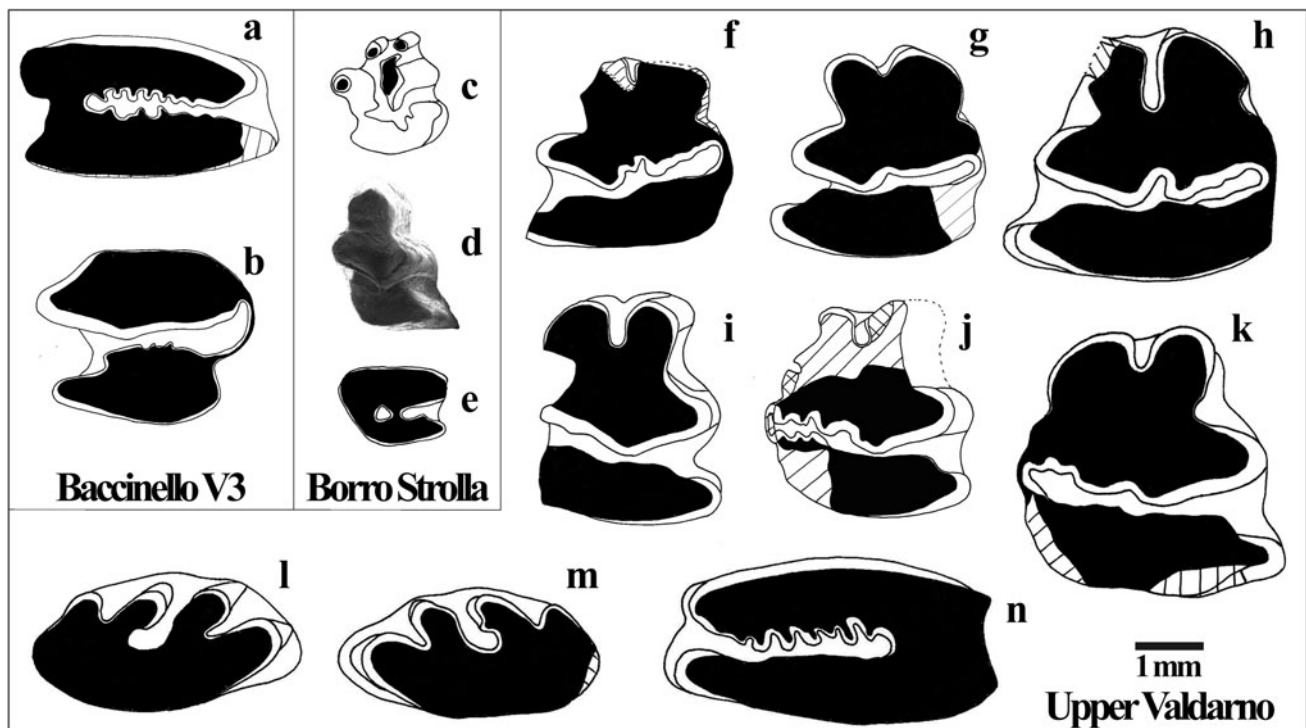


Fig. 5 a P^4 dx NMB 1064, Baccinello V3; b P_4 sin NMB 1062, Baccinello V3. *Trischizolagus* sp.: c P_3 dx IGF 9467V; d D_3 dx IGF 9464V; e M^2 dx IGF 9468V. *Oryctolagus valdarnensis*: f–h P_3 sin

IGF 952, NMB VA1798, IGF 12741; i–k P_3 dx NMB VA2009, IGF 246V, IGF 10129; l P^3 sin IGF 10130; m P^2 sin IGF 946; n P^2 dx IGF 10130

Lower molariforms: P_4 (Fig. 5b) is well preserved, whereas the $m1$ is broken in its anterior and posterior lingual parts; Ltrig = Ltal; the hypoflexid noticeably widens in its lingual part; the anterior side of talonid is crenulated, and a “step” (not a notch) is present in the talonid labial side.

Results

The leporid remains referable to Baccinello V3 curated in NMB do not include highly diagnostic dental positions at the species level as P_3 and, in less extent, P^2 . However, we noticed that the following characters fit in the morphological features that characterize *A. meini*, a taxon typical of the Baccinello V3 faunal assemblage (Angelone and Rook 2011):

1. A peculiar labially enlarged hypoflexus of P^4 ;
2. The crenulation of the talonids in lower molariforms;
3. The lower molariform dimensions.

As for upper teeth dimensions a direct comparison between the original material of *A. meini* (a P^3) and the specimens of NMB (a P^4 and other dental positions posterior to P^3) is not possible. However, the size of NMB specimens is slightly smaller (6–10%) than the P^3 of *A. meini*. The morphological and dimensional characters of

the Baccinello V3 leporids from NMB are therefore compatible with their ascription to *A. meini*.

Genus *Trischizolagus* Radulesco and Samson, 1967

Trischizolagus sp.

Figure 5c–e, measures in Table 1

2008 Leporidae: gen. et sp. indet. Abbazzi et al., p. 620, tab. 1.

2011 *Trischizolagus* Angelone et al., p. 97 (partim).

Locality: Borro Strolla (Valdelsa Basin, Siena), sub-synthem BS-1.

Age: latest Messinian.

Material: M^2 dx: IGF 9468V; D_3 dx: IGF 9464V; P_3 dx: IGF 9467V.

Description

M^2 : (Fig. 5e) young specimen, the distal hyperloph is much smaller than the mesial one; the hypoflexus does not reach the half of the tooth, and bears a spur on the posterior side and posteriorly to it lies a large, triangular fossette.

D_3 : (Fig. 5d) large anteroconid is connected to the trigonid on the labial side; the metaconid is prominent; the

trigonid is connected by a thin isthmus to the talonid; both ento- and hypoconid are slightly undulated in their anterior side.

P₃: (Fig. 5c) almost unworn individual; the anteroconids are two isolated, round islets; also the metaconid is isolated; the protoconid is connected to the talonid by a thin bridge of unworn enamel. The “hypoflexid” has a complex outline, does not reach the lingual side and bends, connecting to the centroflexid. In the “radical” side the conids connected and anteroflexid, protoflexid, paraflexid and metaflexid are formed.

Results

The scanty and badly preserved specimens from Borro Strolla consist in unworn or deciduous teeth. It is not possible to make a reliable comparison of the P₃ from Borro Strolla with other species, even observing the broken “radical” view because the depth of the flexids varies with wear. The D₃ from Borro Strolla has been compared with *T. cf. maritsae* from Alcoy N and Caravaca (Spain, López Martínez 1989) and the leporid from Brisighella known in literature as *T. cf. maritsae* (Gallai and Rook 2011 and references therein; C.A. unpublished data). Its dimensions fall in the lower range of the species. Its large anteroconid and the prominent metaconid fit in the morphology of the material taken as comparison. The M² with a fossette has been observed in large populations of *Trischizolagus* from Spain (C.A. personal database).

These comparisons do not allow taxonomical attribution at the specific level. The early age of the sample (Mio-Pliocene boundary) should exclude an attribution to *T. dumitrescuae*, an eastern European species known since the Early Pleistocene.

Genus *Oryctolagus* Lilljeborg, 1879

Oryctolagus valdarnensis (Weithofer, 1889)

Figure 3f–n, measures in Table 1.

1875 *Lepus* sp. Forsyth Major, p. 39–40.

1876 *Lepus* sp. Forsyth Major, p. 345.

1884 *Lepus* sp. Forsyth Major, p. 2.

1889 *Lepus valdarnensis* Weithofer, p. 55.

1899a *Lepus valdarnensis* Bosco, p. 97–101, pl. XII (II), figs. 3, 5.

1899a *Lepus etruscus* Bosco, 100–101, pl. XII (II), fig. 8.

1899b *Lepus valdarnensis* Bosco, p. 264 (specimens described at points 1^o, 2^o, 3^o).

1899b *Lepus etruscus* Bosco, p. 264–265.

1899 *Caprolagus valdarnensis* Forsyth Major, p. 487.

1954 *Oryctolagus lacosti* Viret.

1971 *Lepus valdarnensis* Forteleoni, p. 36, fig. 1a, 2a, 2c, 3a–1, 5b, tab. 1a, tab. 11a–o.

1972 *Oryctolagus cuniculus* Fondi, p. 9; pl. II. figs. 1–7.

1980 *Lepus valdarnensis* Borselli et al., p. 258.

1984 *Lepus* sp. De Giuli and Torre, p. 123.

1986 “*Lepus*” *etruscus* De Giuli et al., p. 2.

1990 “*Lepus*” cf. *etruscus* De Giuli et al., p. 31.

1989 *Lepus etruscus* López Martínez, p. 217.

1989 *Lepus valdarnensis* López Martínez, p. 217.

1989 *Oryctolagus lacosti* López Martínez, p. 221, 229–230; p. 231, fig. 59.

1992 *Lepus etruscus* Sala, p. 213.

1992 *Lepus valdarnensis* Sala, p. 213.

1997 *Oryctolagus* gr. *lacosti* Gliozzi et al., fig. 2.

2003 *Oryctolagus* cf. *O. lacosti* Girotti et al., p. 89; p. 90, fig. 6c.

2003 *Oryctolagus lacosti* Kotsakis et al., p. 337, 2nd column, line 33.

2003 *Oryctolagus lacosti* Kotsakis et al., p. 337, 2nd column, line 45.

2003 *Oryctolagus* cf. *O. lacosti* Kotsakis et al., p. 338, 1st column, line 9.

2003 *Oryctolagus* cf. *O. lacosti* Kotsakis et al., p. 338, 1st column, line 30.

2003 *Oryctolagus* cf. *O. lacosti* Kotsakis et al., p. 338, 2nd column, line 3.

2003 *Oryctolagus* cf. *O. lacosti* Kotsakis et al., p. 338, 2nd column, line 21.

2009 *Oryctolagus* cf. *O. lacosti* Argenti and Kotsakis, p. 61, fig. 3.

2012 *Oryctolagus* aff. *lacosti* Angelone.

Type: maxillary IGF 946 in Weithofer (1889).

Emended diagnosis: very large size; palatine very reduced and anterior part of choanae enlarged as in *O. lacosti*; P² with deep flexa and hooked loop in the labial side of the paraflexus; P₃ with lingual anteroconid larger than lingual one, often globular labial anteroconid, V-shaped paraflexus, deep, U-shaped anteroflexid, frequent paraflexid.

Geographical distribution: peninsular Italy (Montagnola Senese, Torre Picchio, Upper Valdarno [Olivola FU, Tasso FU], Pietrafitta, Monte Argentario, Pirro Nord).

Chronological distribution: Late Villányan–Early Biharian (Early Pleistocene).

Material: maxillary: IGF 946; IGF 10130; lower jaw sin: NMB VA1798 (with P₃–M₃), IGF 947 (with P₄–M₃), IGF 952 (with P₃–M₂), IGF 12741 (with P₃–M₂); lower jaw dx:

NMB VA2009 (with P_3 – M_2), IGF 246V (with P_3 – M_3), IGF 10129 (with P_3 – M_1).

Description

Upper jaw: long palatal bridge with palatine very reduced; the anterior part ends at the height of the base of P^2 , whereas the posterior part reaches the posterior part of P^4 ; anterior part of choanae wide, posterior part lost.

P^2 : (Fig. 5l–m) developed, V-shaped mesoflexus, deep paraflexus with hooked posterior labial edge; deep hypoflexus; lagicone slightly smaller and less prominent than mesial hypercone.

Upper molariforms: (Fig. 5n) the deep hypoflexus (about 70% of tooth width) is crenulated in its anterior part, and may be undulated in the distal one.

Lower jaw: number and position of foramina variable.

P_3 : (Fig. 5f–k) long anteroconids; the labial anteroconid seems longer than the lingual one except in IGF 12741 (Fig. 5h) and NMB VA1798 (Fig. 5g); the lingual anteroconid is the widest of the two; anteroflexid deep, wide (from the half to the entire length of anteroconids), U-shaped (except in NMB VA1798, in which the anteroflexid is V-shaped in its anterior side and U-shaped in its distal end); in one specimen (IGF 952, Fig. 5f) it can be observed how the shape of anteroflexid changes through ontogeny, from V-shaped to U-shaped; labial anteroconid smaller than lingual one, as large as metaconid; V-shaped, smooth protoflexid, that together with the long anteroflexid “squeezes” the base of the labial anteroconid that may appear globular; deep hypoflexid, from smooth to crenulated in the lingual part (after the centroflexid); centroflexid variable from deep and crenulated to absent (NMB VA2009, Fig. 5i); paraflexid always present, with cement visible at the occlusal surface height (IGF 12741 and NMB VA1798) or starting at a lower part of the tooth shaft; in the posterior part of the hypoflexid, under the centroflexid, the enamel band bends sharply (except in VA 2009) whereas in IGF 10129 it bears a small notch.

Results and comparisons

Historical background and revalidation of *O. valdarnensis* (Weithofer 1889)

The first reports of leporids from Upper Valdarno (attributed to *Lepus* sp.; Forsyth Major 1875, 1876, 1884) were followed by their ascription to a new species, *L. valdarnensis* (Weithofer 1889), eventually split in two species (*L. valdarnensis* and *L. etruscus*, plus postcranial remains referred to *Lepus* sp.; Bosco 1899a, b). Eventually Forsyth Major (1899) attributed all the Upper Valdarno leporid remains to the genus *Caprolagus*. Fifty years later Viret

(1954) recognized them as pertaining to *Oryctolagus* putting them in synonymy with the western European species *O. lacosti*. Such decision was followed since then in literature except by Forteleoni (1971), who attempted to revalidate the species but provided insufficient or wrong iconographic and morphological information, as already remarked by López Martínez (1989).

We agree to assign the Upper Valdarno leporids to the genus *Oryctolagus*. Indeed they show “leporine” characters: very large dental size, comparable to that of *Lepus*, palatal bridge with palatine bone very reduced and wide choanae (at least in the anterior part, the only that can be observed), length of $P_4 < M_2$. However, the validity of the maxillary characters (discriminant of extant *Lepus* and *Oryctolagus*) also for the fossil record was questioned by Viret (1954). Actually the very peculiar rabbit *O. lacosti* (Early Pleistocene of southern part of western Europe, plus isolate findings in Hungary and Greece; López Martínez 1989, 2008) shows such “leporine” maxillary characters. *O. valdarnensis* also shares with some populations of *O. lacosti* a very large size and an overall morphology of P_3 and P^2 that may appear similar at a superficial glance. On the other hand, in spite of a recent revision of material from the type locality (De Marfá and Mein 2007), *O. lacosti* is far from being a well-characterized species, as reflected by its very broad variability.

In our opinion *O. valdarnensis* is a valid species, characterized by the exclusive, contemporaneous presence of the following characters:

1. P_3 with anteroflexid deep (DC1) and parallel-sided (DC2), globular labial anteroconid (DC3), V-shaped protoflexus (DC4); according to Angelone (2012) the contemporaneous presence of these characters distinguished *Oryctolagus* from Pirro Nord and Torre Picchio from other species. It is necessary to remark that Angelone (2012) stated: “The most similar to *Oryctolagus* from Pirro Nord among OOP [= Older *Oryctolagus* populations] from which P_3 is available or well figured is the sample from Torre Picchio, as they share some distinctive characters absent in other OOP.” However, the direct observation of the material from Montagnola Senese and Upper Valdarno revealed that also this material shows such characters and that important details were not described nor correctly figured in the correspondent literature.
2. P^2 with paraflexus hooked in its labial posterior side (here defined as DC5);
3. very large dental size, fairly the largest known for the genus (Fig. 4b).

The observations made in Angelone (2012) to distinguish the population of Pirro Nord (there left in open nomenclature as *O. aff. lacosti*, and here included in

O. valdarnensis) from other congeneric species of the Pleistocene of Europe are valid for *O. valdarnensis* and we thus refer to Angelone (2012) for further details. However, the distinctive characters of *O. valdarnensis* from Upper Valdarno can be summarized as follows: (1) straight anteroflexid; (2) paraflexid with cement always present; and (3) largest size.

We ascribe to *O. valdarnensis* the Late Villányan–Early Biharian Italian populations of *Oryctolagus* (OOP in Angelone 2012): Montagnola Senese (Tuscany, Fondi 1972), Torre Picchio (Umbria, Girotti et al. 2003); Pietrafitta (Umbria, Argenti and Kotsakis 2009), Monte Argentario (Angelone et al. 2008) and Pirro Nord (Angelone 2012). The locality Monte Peglia (Umbria, late Early Biharian, Van der Meulen 1973) was not included in this revision as the material (kept at the Istituto Italiano di Paleontologia in Rome, IsIPU) is at present not available for study. Lacking direct observation, we prefer not to include for the moment in *O. valdarnensis* the fossils from Casa Sgherri (Tuscany, Marcolini et al. 2000) and the old collections of Upper Valdarno housed in the Monteverchi Museum, that could likely pertain to *O. valdarnensis* on a geographical and temporal basis. In Angelone (2012) *Oryctolagus* remains from Upper Valdarno are referred to Olivola FU on the basis of Forteleoni (1971) statements. According to the most recent revision of the Upper Valdarno stratigraphy (Fidolini et al. 2012; Ghinassi pers. com), the Upper Valdarno *Oryctolagus* specimens herein analyzed, including those studied by Forteleoni (1968, 1971) must be referred (when a locality indication is available in the old collections labels) to Upper Valdarno–Tasso FU. The occurrence of *O. valdarnensis* within the Olivola FU is also most probable since (fide Forteleoni 1971), within the Monteverchi collections are housed specimens from “Le Mignaie”, a site correlatable with Castelfranco di Sopra, the type locality for *Mimomys pliocaenicus* (Masini and Torre 1987) and thus Late Villányan (Olivola FU).

We decided to include IGF 952 (Fig. 5f) in *O. valdarnensis* (contra Bosco 1899a, who considers it a separate species under the name of *L. etruscus*), because in the anterior side of its P₃ it can be observed how the anteroflexid changes with wear leading to the typical anterocoinid–trigonid morphology of *O. valdarnensis*. NMB VA1798 (Fig. 5g) was the most problematic specimen due to its particular anteroflexid (compare specimens in Fig. 5). The presence in NMB VA1798 of features characteristic of *O. valdarnensis* as a large labial anteroconid, a V-shaped protoflexid and of features typical of *O. valdarnensis* from Upper Valdarno, as a deep paraflexid with cement, let us in favor to ascribe it to *O. valdarnensis*.

Finally, we prefer not to formally include the Upper Valdarno remains assigned to *Lepus* sp. by Bosco (1899a)

in *O. valdarnensis*, although they may most probably be referred to *O. valdarnensis*. Actually they consist in postcranial material that has not been analyzed in this revision.

Intraspecific variability of O. valdarnensis

The material of *O. valdarnensis* is relatively abundant and most dental positions are represented, as well as a few mandibles, only in Montagnola Senese (MS) and Torre Picchio (TP). Some slight differences distinguish the Upper Valdarno remains here analyzed and those from MS and TP. The first is the lesser average size in both cases. With respect to those from Upper Valdarno, the upper molariforms from MS appear highly crenulated also in the posterior part of the hypoflexus. The P₃ from MS show a more globular labial anteroconid (DC3), due to the labially shifted anteroflexid end (15% of incidence in Upper Valdarno, 60% of worn individuals in MP) and the cement in the paraflexid is much less frequent in MS. It is worth mentioning that the anteroflexid of MS population is U-shaped (DC2) and not V-shaped as figured in Fondi (1972), in which the enamel proportions are also altered. In MS it is possible to observe two juvenile P₃, both with open hypoflexus (as those of *O. laynensis*; López Martínez 1989) and in the younger of the two (unworn) the lingual anteroconid is isolated.

Open hypoflexus and isolated lingual anteroconid are characteristics of the single juvenile individual from TP. What makes the population of TP very peculiar is the retention of a fossette posterior to the hypoflexus in two loose upper molariforms, probably pertaining to the small-aged individual. In addition, in P₃ from TP the hypoflexid is extremely deep, touching the lingual edge of the tooth, the anteroflexid is straight, but always very deep (whereas in Upper Valdarno the depth is more variable), deeper than in MS, and the paraflexid is absent or extremely reduced.

The *Oryctolagus* sample from Pirro Nord (PN) represents a minimal part of a huge collection that is still unavailable for study and may provide complete information about the whole appendicular skeleton of *O. valdarnensis*. In its morphological traits the sample from PN is very similar to those of TP, except for the occurrence in 2/5 specimens of P₃ from PN of a paraflexid (one of the two filled with cement), a more frequent centroflexid, shorter anteroconids, and an even longer hypoflexid that in some cases can be “open”.

In the sole upper jaw from Pietrafitta (figured in Argenti and Kotsakis 2009) it is possible to observe a P² with paraflexus “curl” and upper molariforms with very deep, crenulated hypoflexus, as in *O. valdarnensis*. The only difference with the Upper Valdarno material seems a shallower paraflexus.

A single P² collected in a karst infilling at Monte Argentario, preliminarily classified as Leporidae indet. (Angelone et al. 2008) is probably to be ascribed to *O. valdarnensis*, due to the paraflexus hooked end.

Discussion and conclusions

Taxonomy

The revision of fossil lagomorphs of the latest Neogene–Early Pleistocene of Tuscany housed in the NMB and IGF allows to identify the following lagomorph genera: *Prolagus*, *Alilepus*, *Trischizolagus*, *Oryctolagus*.

Prolagus

This study evidences that a species of *Prolagus*, different from those up to now identified in peninsular Italy (*P. sorbinii* and *P. cf. sorbinii* during Messinian and Early Pliocene, and *P. italicus* during Early Pleistocene; Angelone 2007, 2008 and references therein), is present in the Plio-Pleistocene of Tuscany (Arcille, Solava, Case Inferno). It closely resembles *P. depereti*, “*P. savagei*” and juvenile *P. sorbinii*. At present we prefer to leave it in open nomenclature as *P. aff. sorbinii* due to the taxonomic controversies that involve “*P. savagei*” (see section “Systematic palaeontology”).

Additional data on Italian *Prolagus* are given by the study of *Prolagus cf. sorbinii* from the earliest Messinian and earliest Pliocene of Tuscany (Velona and Borro Strolla). Velona records the oldest report of the genus in the Italian peninsula. *Prolagus cf. sorbinii* from Velona shows similar morpho-dimensional features to the neighboring but younger population of Borro Strolla, with the sample from Maramena (Greece, Mio-Pliocene boundary; de Bruijn 1995) and with *P. sorbinii* Brisighella 6 (central Italy, post-evaporitic Messinian).

Other reports of *Prolagus* from Tuscany in old literature are nowadays unknown in the examined collections, and are here quoted for completeness of this revision.

- The occurrence of *Prolagus* sp. in the Baccinello V3 fauna was reported on the basis of a tentative “dimensional” attribution of a single upper first incisor of quite small size (B. Engesser pers. com. in Rook and Masini 1990). As a matter of fact, such an attribution cannot be confirmed since no trace of the incisor was found in the collections of NMB.
- The most famous “missing *Prolagus* of Tuscany” is the so-called *Prolagus elsanus* (nomen nudum according to López Martínez and Thaler 1975). The original material from Casino, eventually lost, was neither illustrated

nor described (Forsyth Major 1875; Rüttimeyer 1876). Forsyth Major (1899) gave a short description of *P. elsanus* and Tobien (1935) hypothesized its relationship with *P. sardus*. However, Forsyth Major (1899, p. 460–461) mentioned that the P₃ of *Prolagus elsanus* (indicated in the original text as “P₂”) bore a small posterior cusp, that he never observed in other species of the genus. We agree with López Martínez and Thaler (1975) who identified such cusp as a hypoconulid. The hypoconulid is not a feature of the genus *Prolagus*. Thus, the actual presence of *Prolagus* sp. in the Casino fossil assemblage, reported also in relatively recent papers (Rook 1992, table 1 and p. 145; Rook et al. 1999, tab. 10.3) is in all probability incorrect.

- Falconer (1868) reports *Lagomys* (= *Prolagus*) among the vertebrates of Upper Valdarno with no further reference. The presence of *Lagomys* (= *Prolagus*) is confirmed by Forsyth Major (in Stoppani 1872; see also Forsyth Major 1884) but not in later faunal lists of the vertebrates of Upper Valdarno (Forsyth Major 1875, 1876, 1884). In the above mentioned publications there is no reference to repository or inventory numbers thus we do not know if such specimens of *Lagomys* (= *Prolagus*) were lost or if their taxonomic assignment was reconsidered in later lists (actually in later lists the elimination of *Lagomys* coincide with the appearance of *Lepus*). Bosco (1899a, b) finds no trace of *Lagomys* mentioned by Falconer and Forsyth Major, but reports and describes two lower right molariforms of *Lagomys* probably pertaining to the same mandible collected from Upper Valdarno that the IGF acquired in 1887. The specimens (cited also by Tobien 1935) are not figured and are probably lost.

Alilepus

In a recent paper Angelone and Rook (2011) described the Baccinello V3 leporid material from IGF, and recognized it as belonging to a new species named *Alilepus meini*. The analysis of the leporid material from Baccinello V3 from the NMB collections allows us to exclude the occurrence within the Baccinello V3 assemblage of the genus *Hypolagus* as reported in faunal lists since Hürzeler and Engesser (1976) (see synonymic list) and thus confirming our taxonomic conclusions based on more recently collected material housed in the IGF (Angelone and Rook 2011).

Trischizolagus

Borro Strolla is the second Italian report of this quite rare genus after Brisighella (Rook and Delfino 2004, and references therein). The genus possibly occurs also at Moncucco (NW Italy, post-evaporitic Messinian, Angelone

et al. 2011), but the leporid from this locality still lacks a detailed study and a generic attribution.

The taxonomical attribution of the studied *Trischizolagus* material has not been possible at the species level, because the available sample (Borro Strolla) consists of badly preserved, unworn or juvenile teeth. A revision of the Italian record of the genus is in progress.

Oryctolagus

The leporids from Upper Valdarno have a very long story of taxonomic controversies.

We agree with Weithofer (1889), who first described them, that they deserve the rank of independent species but we disagree with their assignment to the genus *Lepus*. Contra Bosco (1899b), we recognize a single species, *Oryctolagus valdarnensis* (Weithofer 1889), being the remains classified as *L. etruscus* an extreme of the morpho-dimensional variability. Six distinctive features characterize the teeth of *O. valdarnensis*: DC1 (deep anteroflexid), DC2 (parallel-sided anteroflexid), DC3 (globular anteroconid), DC4 (V-shaped protoflexus); DC5 (hooked labial side of the paraflexus), and the largest dental size range up to now reported in the genus.

We assign to *Oryctolagus valdarnensis* the Upper Valdarno leporids and those from the Late Villányian–Early Biharian local faunas of Montagnola Senese, Torre Picchio, Pietrafitta, Monte Argentario and Pirro Nord. Lacking direct observation, for the moment we prefer a cautious solution and we prefer not to include in the species *O. valdarnensis* the fossils from Casa Sgherri (Lower Valdarno), Mignaia (Upper Valdarno) and Monte Peglia. It is likely that the leporids from Casa Sgherri and Mignaia are *O. valdarnensis*, due to their geographical and temporal localizations. In Monte Peglia the taxonomic framework is more complex (both *Oryctolagus* and *Lepus* remains were reported, even if probably from different levels; Van der Meulen 1973); Monte Peglia is the last *Oryctolagus*-bearing Italian locality before a temporal gap in the Italian fossil record of the genus *Oryctolagus* in the Late Biharian (Angelone 2012), coeval to the first reliable record of *Lepus* in Italy. Thus, Monte Peglia is it a key site to understand the history and the evolution of Italian leporids. Unfortunately the material is at present not available for study.

The reports of “*L. valdarnensis*” out of the Italian peninsula (Romania, Simionescu 1932; Macarovici 1978 and references therein) were incorrect as they pertain to *Trischizolagus dumitrescuae* (Radulesco and Samson 1967).

Evolutionary trends and palaeobiogeography

The characters of *Prolagus* cf. *sorbinii* from Velona and Borro Strolla are similar to the specimens from Maramena

(Greece, Mio-Pliocene boundary, de Bruijn 1995) and *P. sorbinii* Brisighella 6 (central Italy, post-evaporitic Messinian). These features, characterizing samples of Messinian age, can be considered as fluctuations around a “classic” morphotype probably driven by palaeoecological conditions.

It is interesting to notice the co-occurrence of *Prolagus* cf. *sorbinii* and *Trischizolagus* sp. from the same subsynthem (BS-1) at Borro Strolla referable to the latest Messinian (Abbazzi et al. 2008). A feature in common with other latest Messinian sites known in Italy, Brisighella and, possibly, Moncucco.

Prolagus aff. *sorbinii* shares with *P. italicus* three among four of characters typified for the P₃ of Plio-Pleistocene species of *Prolagus* of the Italian peninsula that distinguish them from western European coeval species (Angelone 2008): a thick entoconid, no entoconid enamel hiatus, size enlargement. The fourth character, the enamel crenulation and the retention of crochet, observed in *P. italicus* but not in *Prolagus* aff. *sorbinii* should be eliminated from the list of typical characters of Italian Plio-Pleistocene *Prolagus* species. Actually enamel crenulation can be observed in some non-insular geographically restricted species of prolagids (*Ptychoprolagus forsthartensis* and, in a less extent, *P. laynensis*; Angelone 2005, see figures in Tobien 1975; López Martínez and Thaler 1975).

Evidently, *Prolagus* aff. *sorbinii* had a wider geographical distribution than *P. italicus* (known only from two sites in central Apennines; Angelone 2008). For the moment it is not possible to define it with certainty, but if *Prolagus* aff. *sorbinii*, “*P. savagei*” and *P. depereti* are all belonging to the same species, with a distribution that includes at least north-western and central Italy and southern France.

Alilepus meini is one of the several large and small mammal species of the Early Messinian of southern Tuscany with a geographically restricted range (see Angelone and Rook 2011 and references therein). The evolutionary tendencies in dental pattern of leporids in non-insular geographically restricted environments is not known, but at least for *Alilepus* it seems to parallelize that of some ochotonids (Angelone 2005, see above) as its teeth show more crenulated/undulated enamel with respect to wider-ranging species, not coupled to size increase.

As mentioned above, concerning *Trischizolagus* sp., a revision of the leporids of the late Messinian of Italy (Brisighella and Moncucco) is pending. At present it is not possible to have a firmer taxonomic attribution and, consequently, to delineate hypotheses on the evolutionary tendencies and temporal and geographical distribution of this taxon.

The geographical distribution of the leporid *Oryctolagus valdarnensis* is also limited to the Italian peninsula during

the Late Villányian–Early Biharian. Its appearance in the time equivalent to the Costa San Giacomo FU (2.3–2.1 Ma according to Sala and Masini 2007, and Rook and Martínez-Navarro 2010) follows that of *O. lacosti* in western Europe (≈ 2.5 Ma; López Martínez 2008). In central Italy the distribution area of *O. valdarnensis* overlaps that of *P. italicus* (actually *O. valdarnensis* is present in both Montagnola Senese and Torre Picchio), and that of the younger samples of *P. aff. sorbinii* (Upper Valdarno). In southern Italy (Pirro Nord) *O. valdarnensis* is found together with *Hypolagus*, although Angelone (2012) casts doubts on their actual temporal co-existence.

The differences noticed among the populations of *O. valdarnensis* may be due to different factors. If we consider the Upper Valdarno examined specimen of Tasso FU as a composite “population”, we notice temporal trends in P_3 towards:

1. Elongation of the hypoflexid, leading to a “open” hypoflexid in some specimens of Pirro Nord, that represents the retention of a juvenile character observed in Montagnola Senese and Torre Picchio.
2. More detached, smaller labial anteroconid if compared to lingual one.
3. A higher incidence of an anteroflexid as long as the anteroconids, also due to the shortening of the anteroconids.

Other features, such as the incidence of centroflexid, do not follow a precise trend and may be controlled by local factors (environment or interaction with other species). The degree of crenulation of the lingual side of the hypoflexid, and the incidence of paraflexid seem to follow a geographical trend (Torre Picchio and Pirro Nord, placed in a more southern geographical position, both lack crenulation and paraflexid).

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Appendix 1

List of fossil material included in *O. valdarnensis* (Weithofer 1889) in addition to NMB and IGF Upper Valdarno specimens mentioned in the “Systematic palaeontology” section.

Montagnola Senese

Repository: Coll. Fondi, Dipartimento di Scienze della Terra, Università di Siena (Italy); prefix: IGPS

Material: **incisors** 154, 154a, 154b, 155, 156, 157, 158, 158a, 158b; **P²** 146, 147, 148, 149, 227; **upper molariforms** 150, 151, 152, 153, 164, 165, 166, 167, 168, 169, 174, 179, 225, 226, plus 25 (previously classified as *Prolagus*); **lower jaws** 174, 178 (a composite of two mandibles, the anterior one (178a) with P_3 – M_1 , the posterior one (178b) with M_1 – M_3); **P₃** 170, 171, 172, 173, 175, 176, 177, 177a; **lower molariforms** 159, 160, 161, 162, 163, plus 29, 31 and 32 (previously classified as *Prolagus*).

In the specimens figured in Fondi (1972, pl. II, figs.1–7) the inventory numbers of the following specimens is different: 173 is reported as 169 (now assigned to a lower jaw); 175 is reported as 174 (now assigned to a lower jaw).

Torre Picchio

Repository: Mostra permanente “ex Chiesa di San Tommaso”, Terni.

Material: **upper molariforms** 6.4, 6.5, 6.6, 7.2, 8.2, 8.3, 9.3; **P²** 8.1; **lower jaw** 10.1; **P₃** 6.7, 9.2, 11.1; **lower molariform** 6.8.

Pietrafitta

Repository: ENEL Thermoelectric Station “Città di Roma”, Pietrafitta.

Material: **upper jaw** 1907.

Monte Argentario

Repository: Dipartimento di Scienze della Terra, Università di Torino; prefix: PU.

Material: **P²** 463

Pirro Nord

Repository: Dipartimento di Scienze della Terra, Università di Torino; prefix: PU.

Material: P² 126999 (fissure 10F); P₃ 126993, 126994 (fissure 10A), 126995, 126997, 126996, 126998 (fissure 10F).

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