

FOSSIL LAGOMORPHA (MAMMALIA) OF ITALY: SYSTEMATICS AND BIOCHRONOLOGY

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Abstract. Revisions performed in the last 15 years added remarkable novelties to the taxonomy and biochronology of Italian fossil lagomorphs. Several new taxa have been erected basing on new materials and on the revision of old materials. This paper aims to illustrate the state of the art of such researches. The lagomorph diversity in the Italian Neogene and Pleistocene is quite high, accounting 9 ochotonids, 14 leporids, and 3 stem lagomorphs. Among the lagomorph taxa recorded in Italy, quite a high number are insular or continental endemics. The oldest Italian lagomorphs are the insular endemic *Paludotona* aff. *minor*, *P. etrusca* and *P. minor* from the early-middle Turolian of the Tusco-Sardinia palaeobioprovince, and *Prolagus apricenicus* and *P. imperialis* from the late Turolian of the Abruzzi-Apulia palaeobioprovince. In the Italian peninsula, lagomorphs are known since the late Turolian (early Messinian). *Prolagus* appears in pre-evaporitic Messinian (*Prolagus sorbinii*) and gives rise to species endemic to the Italian peninsula (*Prolagus italicus*, late Villányian, central Italy; *P. savagei*/*P. aff. sorbinii*, early Villányian-early Biharian, NW and central Italy). The presence of *Prolagus* was probably constant until the early Biharian, age of its latest report in the Italian peninsula. The gap in the Pliocene fossil record is apparent and due to the extreme scarcity of fossil localities bearing continental vertebrates in the Italian Pliocene. The Asian genus *Ochotona* appeared at least twice in the Middle-Late Pleistocene of NE Italy, in correspondence of cold climatic phases. *Prolagus* of the latest Miocene-Early Pliocene of Italy represents the stock which originated the Sardinian lineage of *Prolagus*. The Sardinian species of *Prolagus* form an endemic insular anagenetic lineage whose oldest element is the earliest Late Pliocene *P. aff. figaro*, and which persists till historical times. The main turnover in the lineage, i.e. the transition *P. figaro*-*P. sardus*, is an event possibly related to the Mid-Pleistocene Transition. Minor morphological and dimensional changes can be detected among the population of both *P. figaro* and *P. sardus*, allowing a relative chronological arrangement of the *Prolagus*-bearing fossil sites. The first Italian leporids appear in the late Turolian. The continental endemic *Ailepus meini* is limited to the pre-evaporitic Messinian of Tuscany, and *Trischizolagus* sp., a taxon that still lacks a detailed systematic revision, is known from a couple of evaporitic and post-evaporitic Messinian fossil localities of northern-central Italy. There are no leporids in the Italian fossil record between the earliest Pliocene and the Late Pliocene (early Villányian), i.e. before the oldest Italian record of *Hypolagus*. This genus is represented by scanty remains pertaining to different species, and is distributed all along the peninsula (*H. petenyii*, early Villányian, NW Italy; *H. brachygnathus*, earliest Biharian, NE Italy; the continental endemic *H. aff. brachygnathus*, early Biharian, SE Italy). In Sicily, *Hypolagus* is present with an endemic insular species (*H. peregrinus*, ?late early Biharian). Also Sardinia records an endemic insular leporid, *Sardolagus obscurus* (Early Pleistocene). Its morphological features underwent significant modifications due to the permanence in an insular environment, preventing for the moment reliable phylogenetic inferences aimed to link it to known European continental genera. Extant lagomorph genera arrive in Italy with some delay with respect to the rest of Europe. In Europe, *Oryctolagus* is known since the Late Pliocene, whereas the oldest Italian species, *O. valdarnensis*, is known from the Early Pleistocene (late Villányian-early Biharian) of central and probably SE Italy. After a gap in the late Biharian, *Oryctolagus* is recorded in the earliest Toringian of NW and western-central Italy with *O. burgi*. The extant species *O. cuniculus* appears in the Italian peninsula in the late Middle Pleistocene. Its presence is attested until MIS 3 in several Italian fossil sites, and in the MIS 2 and early Holocene in southernmost Italy, Sicily, and southern Italian minor islands. It can not be excluded that those relict populations interacted with the rabbits introduced by humans during the Holocene. As for *Lepus*, the oldest reliable Italian report dates back to the late early Biharian of central Italy (originally classified as *L. terraerubrae*). Extant species of *Lepus* appear in Italy since the early Toringian. Among them, *Lepus corsicanus* has the oldest record; this species expands its geographical distribution to Sicily in the latest Pleistocene. Follows *L. europaeus*, whose oldest reliable Italian record is in the earliest late Toringian; this species expanded in the Italian peninsula at the expenses of *L. corsicanus*. During the Last Glacial Maximum, *L. timidus* makes sporadic appearance(s) in Italy, even in southern regions. Though showing endemic characters, the Sardinian hare *L. mediterraneus* is the result of human introduction in historical times.

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INTRODUCTION

Lagomorphs represent a very important, diverse, and abundant component of European small mammal assemblages since Miocene on. In the last two decades, a renewed interest in European fossil lagomorphs led to the revision of several Italian lagomorph taxa (Angelone 2007, 2008a, 2013; Angelone & Rook 2011, 2012; Angelone et al. 2008, 2015, 2017, 2018 among others). We provide here: (1) an update of the systematics of Italian lagomorphs since their first appearance in the Italian territory (Late Miocene) to the Holocene; (2) their phylogenetic affinities, when possible; (3) a synthesis of the biochronological history of Italian lagomorphs of each different bioprovinces, starting from the early-middle Turolian; and finally (4) we pinpoint the research perspectives and the open questions emerged after this review.

MATERIAL AND METHODS

The sources of the data here illustrated are published references or unpublished material currently under study. An iconographic overview of the Italian lagomorph taxa is given in Figs. 1-2.

A list of late Turolian-Biharian fossil lagomorphs of Italian mainland, supplied with taxonomic details, geographical distribution, age, and references is given in Tab. 1. For Toringian, we selected among the numerous reports available in literature, those publications in which there is at least a description/discussion of the lagomorph taxa in the text. As for insular assemblages, the list of fossil lagomorphs retrieved in insular endemic domains which are today part of mainland Italy (the Tusco-Sardinia and the Abruzzi-Apulia palaeobioprovinces; Kotsakis et al. 1997; Rook et al. 2006) is reported in Tab. 1, whereas fossil lagomorphs of Italian islands are listed in Tab. 2.

The taxonomy of lagomorph remains recorded in insular palaeobioprovinces is illustrated together with the fossil lagomorphs of Italian mainland. The lagomorphs from Italian islands are discussed in separate sections.

The chronological distribution of Italian lagomorph taxa is illustrated in Fig. 3 (mainland Italy), and in Fig. 4 (Sicily and Sardinia). The partition in Mammal Ages and Faunal Units of the Italian Plio-Pleistocene follows Gliozzi et al. (1997), integrated with Petronio and Sardella (1999). Latest criticisms and proposals of modification/integration (e.g. Raia et al. 2005, 2006; Palombo & Sardella 2007; Petronio et al. 2007, 2019; Sardella & Palombo 2007; Palombo 2014, 2018a; Bellucci et al. 2015) are to be accepted only after a revision of the huge amount of new data collected in the XXI century, combined with the revision of older data.

The age of the fossiliferous sites of peninsular Italy follows Kotsakis et al. (2003), Masini and Sala (2007, 2011), Sala and Masini (2007), or specific publications cited in the text. For Sardinia, we follow Palombo (2006, 2009, 2018b), and Palombo and Rozzi (2014). For Sicily, we follow the scheme originally proposed by Kotsakis (1979), eventually modified by Bonfiglio and Kotsakis (1987) and Bonfiglio et al. (2002), in its latest version proposed by Marra (2013).

In the text, we used the following abbreviations:

BV0, BV1, BV2, BV3: Baccinello local biochron V0, V1, V2, V3

FC, FsC: Faunal Complex, Faunal sub-Complex

FU: Faunal Unit

IsIPU: Istituto Italiano di Paleontologia Umana

NHMB: Naturhistorisches Museum Basel

PB: palaeobioprovince

TAXONOMIC OVERVIEW OF FOSSIL LAGOMORPHS OF ITALIAN MAINLAND

Early-middle Turolian (MN11-12, Late Miocene)

Paludotona Dawson, 1959

The endemic insular genus *Paludotona* is the oldest known Italian lagomorph. *Paludotona* was considered an ochotonid in older literature, but recent data suggest instead its relationship with stem lagomorphs, the basal group which includes primitive lagomorphs (Angelone et al. 2017).

Paludotona etruria Dawson, 1959 (Fig. 1.a) was reported from Tuscany (at that time part of the insular domain known as the Tusco-Sardinia PB), in horizons referable to BV1 (MN11). Another species of the genus, *Paludotona minor* Angelone, Čermák & Rook, 2017 (Fig. 1.b) was recognized in BV2 (MN12, and possibly earliest MN13, magnetostratigraphically correlated to ~7.1-6.7 Ma; Rook et al. 2011; Benvenuti et al. 2015). The scanty remains of *Paludotona* recently recovered from BV0 (MN11, magnetostratigraphically correlated to ~8.3-8.1 Ma; Rook et al. 2011; Benvenuti et al. 2015) were classified as *Paludotona* sp. by Cirilli et al. (2016). Angelone et al. (2017) noticed that *Paludotona* from BV0 appeared morphologically similar to *P. minor* from BV2, rather than to *P. etruria* from BV1 which is chronologically closer, and decided to ascribe those remains to *P. aff. minor*. *Paludotona* is absent from BV3 continental assemblages, deposited after the re-establishment of the connection with mainland, which persists up to date.

Though abundant in Tuscany, *Paludotona* is not known from Fiume Santo, the sole fossiliferous locality of the Tusco-Sardinia PB located in Sardinia, possibly coeval to V2 horizon of the Baccinello-Cinigiano Basin (Abbazzi et al. 2008a; Casanovas-Vilar et al. 2011).

Late Turolian (MN13, latest Miocene)

Prolagus Pomel, 1853

Remains of the ochotonid *Prolagus sorbinii*

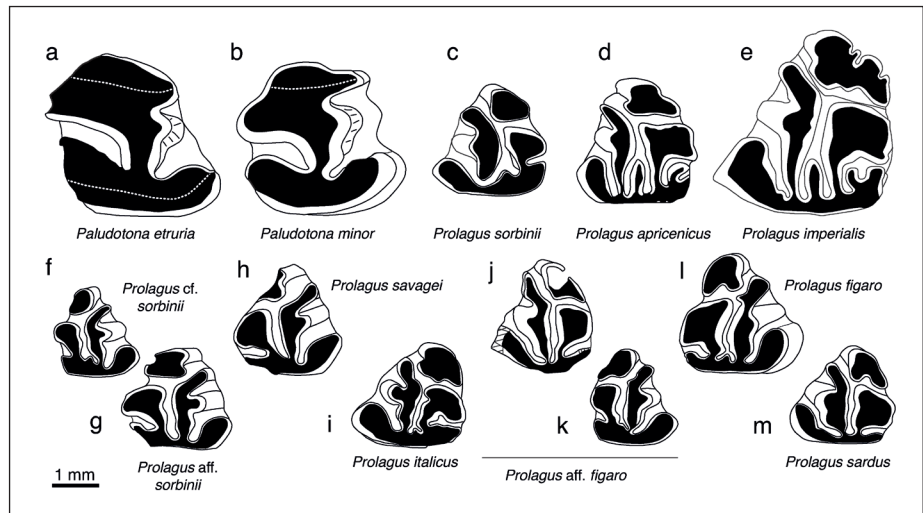


Fig. 1 - Fossil stem lagomorphs and ochotonoids of Italy. a) *Paludotona etruscia*, p3 dx (Baccinello V1; fig. 2C, p. 461 in Angelone et al. 2017); b) *Paludotona minor*, p3 dx (Baccinello V2; fig. 2I, p. 461 in Angelone et al. 2017); c) *Prolagus sorbinii*, p3 sin (Monte Castellaro; fig. 3c, p. 410 in Angelone 2007); d) *Prolagus apricenicus*, p3 sin (Gargano fissure infilling F8; pl. 1.26, p. 235 in Mazza 1987, reversed); e) *Prolagus imperialis*, p3 sin (Gargano fissure infilling F32; pl. 3.4, p. 239 in Mazza 1987); f) *Prolagus cf. sorbinii*, p3 dx (Borro Strolla; fig. 3e, p. 132 in Angelone & Rook 2012); g) *Prolagus aff. sorbinii*, p3 dx (Arcille; fig. 3o, p. 132 in Angelone & Rook 2012); h) *Prolagus savagei*, p3 dx (Arondelli; CA, unpublished data); i) *Prolagus italicus*, p3 sin (Montagnola Senese; fig. 2a, p. 448 in Angelone 2008a); j) *Prolagus aff. figaro*, p3 sin (Capo Mannu D1; fig. 2A, p. 290 in Angelone et al. 2015); k) *Prolagus aff. figaro*, p3 dx (Capo Mannu D1; fig. 2B, p. 290 in Angelone et al. 2015); l) *Prolagus figaro*, p3 dx (Monte Tuttavista X4; CA, unpublished data); m) *Prolagus sardus*, p3 sin (Monte Tuttavista V16; fig. 3e, p. 113 in Angelone et al. 2008).

Masini, 1989 (Fig. 1.c), or of closely related forms (*P. cf. sorbinii*), are present in Velona (pre-evaporitic Messinian, Tuscany), Monte Castellaro (evaporitic Messinian, Marches, type locality of the species), and in the post-evaporitic Messinian localities Brisighella (Romagna), Ciabòt Cagna (Piedmont), Moncucco (Piedmont), Verduno (Piedmont) (see Masini 1989; Ghetti et al. 2002; Angelone 2007; Angelone & Cavallo 2010; Angelone et al. 2011; Angelone & Rook 2012; Colombero et al. 2014, 2017). *Prolagus* remains from the post-evaporitic Messinian locality Cava Stingeti (Molise; Cosentino et al. 2018) do not have a specific attribution yet.

Recent surveys in the NHMB (CA, October 2015), led to the re-discovery of an upper first incisor collected in levels referable to BV3 (pre-evaporitic Messinian), whose size and overall appearance are compatible with *Prolagus*. Such specimen was first mentioned in Rook and Masini (1990), quoting a personal communication of B. Engesser. The specimen was not found in a previous survey of NHMB material (see Angelone & Rook 2012: 140), thus, its existence could not be officially re-confirmed until now.

The search of the remains attributed to *Prolagus elsanus* Major, 1899, recovered in the second sedimentary cycle of Casino (Tuscany, late Messini-

an, according to Abbazzi et al. 2008b), was less fortunate. The presence of *Lagomys* G. Cuvier, 1800 at Casino was first reported by Major (1875, part I: 39). In part II of the same paper (Major 1875, part II: 238), the author introduced *Myolagus elsanus* (= *Prolagus elsanus*). Those remains were not figured nor described in the above mentioned paper. A short morphological description of *P. elsanus* was given in Major (1899). However, such description mentions features which have been lost after the earliest Miocene in the lineage leading to the genus *Prolagus* (Angelone & Rook 2012), thus deepening the mystery around the lagomorph from Casino. At present, the remains of *P. elsanus* seem to be lost.

In the late Turolian, two endemic insular species of *Prolagus* were present in the Abruzzi-Apulia PB (now part of the Italian peninsula): *Prolagus apricenicus* Mazza, 1987 (Fig. 1.d), and *Prolagus imperialis* Mazza, 1987 (Fig. 1.e). Remains of both species are yielded in several karst fissure infillings located in the Gargano peninsula (Apulia). However, they have been recovered together only in the most recent among the Gargano infillings accumulated during the Neogene (Masini et al. 2010). The dental morphology and size of *P. imperialis* are highly modified following a specific pattern recognized in insular endemic congeneric species (Angelone 2005).

The available populations of *P. apricenicus*, on the other hand, show quite variable dental morpho-dimensional traits, ranging from smaller forms whose morphology is almost non-modified with respect to continental ones, to larger specimens in which marked insular endemic morphological modifications can be observed (Mazza 1986a, 1986b, 1987; Mazza & Zafonte 1987; Angelone 2005). There is no final accordance about the phylogenetic relationships between the two species: they may be either related by an ancestor-descendant relationship, or they may be two sister species developed from a common ancestor in different islands of the Gargano palaeoarchipelago. Indeed, the “sudden” appearance of *P. imperialis* and the lack of a transitional form between the two species, are elements in favour of the second hypothesis. Cladistic analyses confirm the hypothesis raised by Mazza (1987), and supported by Angelone and Čermák (2015), that the continental ancestor of *P. apricenicus* and *P. imperialis* may be a still not described species close to *Prolagus oeningensis* (König, 1825) pertaining to an eastern European clade of *Prolagus* (Angelone et al. 2015).

It is worth to remark that *P. apricenicus* has been the starting point of a palaeobiological approach to the study of European lagomorphs. The results illustrated in Moncunill-Solé et al. (2015, 2016a) predict a mass of 280 g for *P. apricenicus* from Cava Dell’Erba (F1 site), and of 600 g for the population of the same species from Cava Fina (F8 site). The skeletochronology of the former population (F1) indicates a longevity of at least 7 years, suggesting for *P. apricenicus* a slower life history than expected from body size, when compared with extant ochotonids.

An articulate skeleton of *Prolagus* was recovered in marine sediments in Capo di Fiume (Abruzzo), an area that in the Late Miocene pertained to the Abruzzi-Apulia PB (Mazza et al. 1995). A lower age constraint to the lower Messinian is provided by forams and molluscs. The remains have been tentatively attributed to *P. cf. apricenicus* on the basis of palaeogeographical evidences (Mazza et al. 1995). In fact, observations of the teeth occlusal surface are not possible at present.

Alilepus Dice, 1931

Alilepus is the oldest leporid recorded in the Italian peninsula. *Alilepus meini* Angelone & Rook, 2011 (Fig. 2.a) has been reported from early Mes-

sinian assemblages corresponding to BV3 (magnetostratigraphically dated at ~6.7-6.4 Ma; Rook et al. 2011). In spite of belonging to a balanced, continental faunal assemblage, *A. meini*, as well as other elements of BV3, is a taxon endemic to southern Tuscany not inherited from the endemic Tusco-Sardinia PB. *Alilepus meini* is likely to be related to *Alilepus turolensis* López Martínez, 1977, a species reported from NE Spain and Greece in MN12-14 (Angelone & Rook 2011 and references therein). The erection and description of *A. meini* allowed to definitively discard the presence of *Hypolagus* Dice, 1917 in BV3, hypothesized in literature older than Angelone and Rook (2012: 135, see references in synonymic list). No other report of *Alilepus* is known in the Italian peninsula after the early Messinian.

Trischizolagus Radulesco & Samson, 1967

A leporid reported from Brisighella was originally classified as *Trischizolagus cf. maritsae* Bruijn, Dawson & Mein, 1970 (De Giuli 1989; Rook et al. 2015 and references therein). No description nor illustration of the material is available at present. Pending a systematic revision, we address such materials as *Trischizolagus* sp. basing on preliminary observations by CA (2019). Remains ascribed to *Trischizolagus* sp. (Fig. 2.b) recovered in the lower sub-synthem of Borro Strolla (Tuscany, latest Messinian), consist of unworn, juvenile teeth, and were not determinable at the specific level due to the scantiness and bad preservation of the specimens (Angelone & Rook 2012). In the Italian peninsula, *Trischizolagus* seems not to survive the Mio-Pliocene boundary.

Leporidae indet.

Undetermined leporids have been reported from the late Messinian fossiliferous sites of Moncucco and Cava Stingeti (Angelone et al. 2011; Colombero et al. 2017; TK, pers. data).

Ruscinian-early Villányian (MN14-16, Pliocene)

Prolagus

Prolagus cf. sorbinii (Fig. 1.f) is present in the upper sub-synthem of Borro Strolla, dated to the Messinian/Zanclean transition (earliest MN14; Abbazzi et al. 2008b; Angelone & Rook 2012). The following reports of *Prolagus* in the Italian Penin-

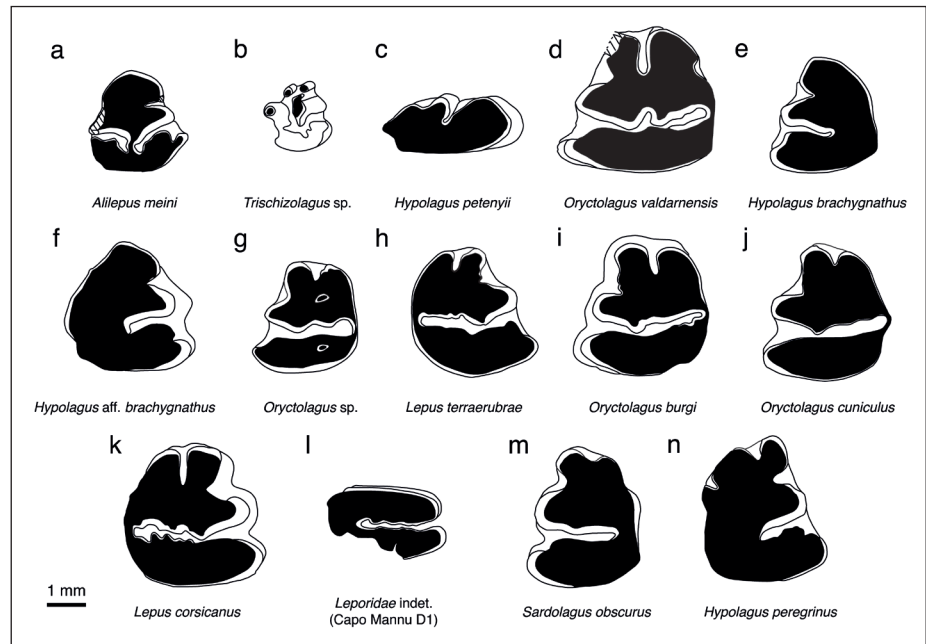


Fig. 2 - Fossil leporids of Italy. a) *Alilepus meini*, p3 dx (Baccinello V3 localities; fig. 2a, p. 153 in Angelone & Rook 2011); b) *Trischizolagus* sp., p3 dx (Borro Strolla, lower sub-synthem; fig. 5c, p. 136 in Angelone & Rook 2012); c) *Hypolagus petenyii*, P2 dx (Aronelli; CA, unpublished data); d) *Oryctolagus valdarnensis*, p3 sin (Upper Valdarno; fig. 3h, p. 132 in Angelone & Rook 2012); e) *Hypolagus brachygnathus*, p3 sin (Monte La Mesa, fig. 3.8, p. 92 in Marchetti & Sala 2002); f) *Hypolagus* aff. *brachygnathus*, p3 dx (Pirro Nord, unknown fissure; fig. 2e, p. 97 in Angelone 2013); g) *Oryctolagus* sp., p3 sin (Monte Peglia, upper levels, fig. 9a, p. 27 in Van der Meulen 1973); h) *Lepus terraerubrae*, p3 dx (Monte Peglia, lower levels, fig. 8 dx, p. 27 in Van der Meulen 1973); i) *Oryctolagus burgi*, p3 sin (Borgio Verezzi, fig. 2-Val 90 27a/3b, p. 21 in Nocchi & Sala 1997a); j) *Oryctolagus cuniculus*, p3 sin (San Sidero 3; fig. 2-MP232-sx, p. 173 in Nocchi & Sala 1997b); k) *Lepus corsicanus*, p3 dx (La Grave; fig. 5A, Kotsakis et al. in press); l) Leporidae indet., right upper molariform (Capo Mannu D1; fig. 2V, p. 290 in Angelone et al. 2015); m) *Sardolagus obscurus*, p3 sin (Monte Tuttavista IVm; fig. 3.1, p. 510 in Angelone et al. 2018); n) *Hypolagus peregrinus*, p3 dx (Monte Pellegrino; fig. 2d and 2f, p. 42 in Fladerer & Fiore 2003).

sula are dated to MN16a. They are *P. aff. sorbinii* from Arcille (Tuscany) (Fig. 1.g) and *Prolagus savagei* Berzi, 1967 from Arondelli (Piedmont) (Fig. 1.h).

Prolagus aff. *sorbinii*, though showing morphological similarities to *P. sorbinii*, is an independent species whose formalization depends on the reassessment of *P. savagei*. Actually, *P. aff. sorbinii* and *P. savagei* are likely to pertain to the same species (Angelone & Rook 2012), however, *P. savagei*, which should have nomenclatorial priority, does not have a clearly stated diagnosis and its supposed distinctive characteristics are confusing and contradictory (see Berzi 1967). Its validity was questioned by López Martínez and Thaler (1975), who listed the species of *Prolagus* known at the time (*ibid.*: 851-852), commenting also on the nomenclatorial/taxonomic problems related to some of them. In the case of *P. savagei*, they argued that the species was based on a fossilization anomaly. Indeed, they did not list it in the species of *Prolagus* they considered as valid (*ibid.*: 852). Nevertheless, they did not literally declare *P. savagei* as invalid, and they did not

put it in synonymy with any of the species reputed as valid. This latter point was questioned by Azzaroli (1977), who instead supported the validity of *P. savagei*. *Prolagus savagei* was eventually synonymized with *Prolagus calpensis* Major, 1905 (Alberdi et al. 1997). Angelone and Rook (2012), however, rejected the synonymy with *P. calpensis*, listing several characters to differentiate *P. savagei* + *P. aff. sorbinii* from *P. calpensis* (*ibid.*: 135).

Hypolagus Dice, 1917

A tooth referable to the genus *Hypolagus* found in Arondelli was at first classified as *Hypolagus* sp. (Berzi 1967), and eventually ascribed to *Hypolagus petenyii* Čermák & Fladerer in Čermák, 2009 (Fig. 2.c). The specimen from Arondelli represents the sole report of the genus in the Italian Peninsula before Pleistocene times.

Late Villányian (MN17, Early Pleistocene)

Prolagus

The continental endemic species *Prolagus*

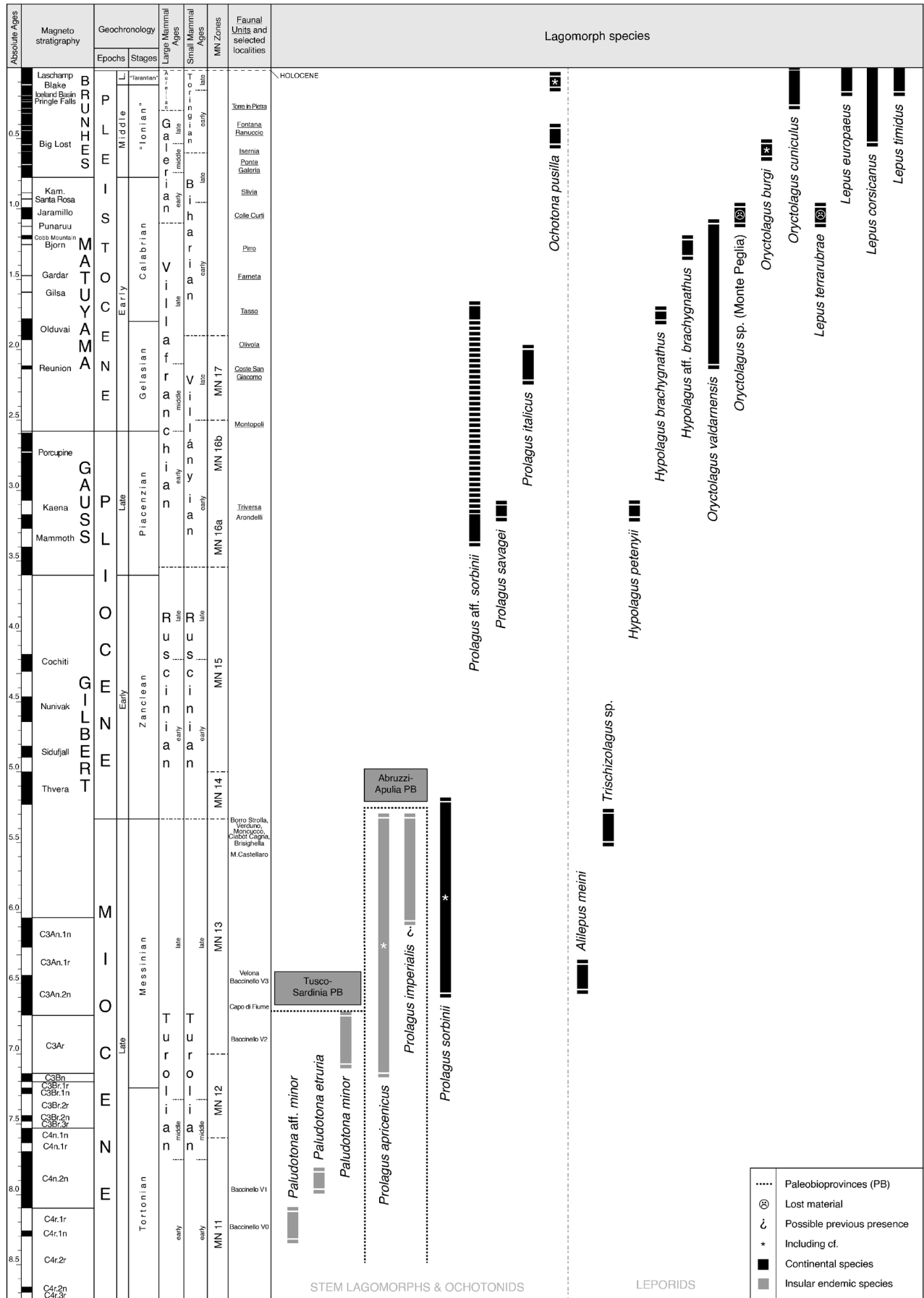


Fig. 3 - Chronological distribution of lagomorph taxa in mainland Italy. Integrated chronology (Geochronology/Magnetostratigraphy, Large Mammal Ages, Small Mammal Ages, MN Zones, Italian FU, and selected fossil localities) modified from Mein (1975), Sala and Masini (2007), Masini and Sala (2011), Hilgen et al. (2012), Colombero et al. (2014).

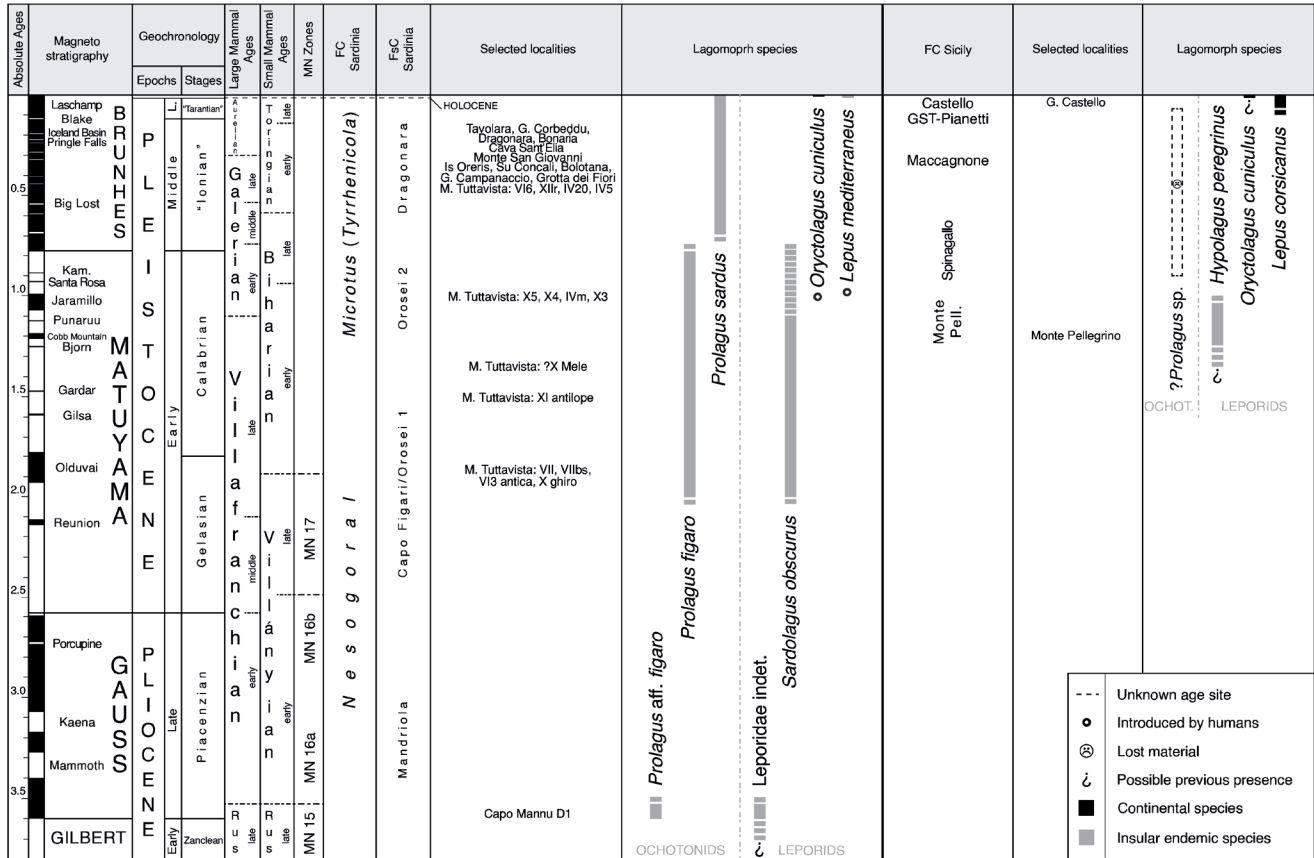


Fig. 4 - Chronological distribution of lagomorph taxa recorded in Sicily and Sardinia. A relative chronological arrangement of some infillings of Monte Tuttavista has been proposed on the basis of the lagomorph content (Angelone et al. 2008, 2009). However, such arrangement takes into account only a part of the fissures containing *Prolagus*. Thus, we decided to group the selected localities in clusters without an internal chronological arrangement. The clusters are arranged in relative chronological order and, when possible, next to the correspondent FC following Palombo (2009). The relative chronological position of most Capo Figari infillings is doubtful due to taphonomic mixing/sampling bias, thus we do not report them here. Integrated chronology (Geochronology/Magnetostratigraphy, Large Mammal Ages, Small Mammal Ages, MN Zones, Sardinian and Sicilian FC, and selected fossil localities) modified from Mein (1975), Bonfiglio et al. (2002), Masini et al. (2008), Palombo (2009), Hilgen et al. (2012), Marra (2013). GST-Pianetti: Grotta San Teodoro-Pianetti. FC Monte Pell.: Monte Pellegrino FC.

italicus Angelone, 2008 (Fig. 1.i) has been erected basing on fossil material from Montagnola Senese (Tuscany, Coste S. Giacomo FU; Fondi 1970). In the same paper, were attributed to *P. italicus* also the *Prolagus* remains from Torre di Picchio (Umbria, Olivola FU; Girotti et al. 2003). Recent researches highlight the presence of *P. italicus* in the Coste S. Giacomo fossil locality (Latium, Coste S. Giacomo FU; Bona et al. 2015). This discovery slightly pre-dates the appearance of *P. italicus* with respect to older literature. Cladistic analyses suggest that *P. italicus* developed from *P. sorbinii* “immediately” after its arrival in the Italian peninsula in the early Messinian (Angelone et al. 2015). Being derived from *P. sorbinii*, *P. italicus* is the sister species of *P. savagei*/*P. aff. sorbinii*.

Other remains of *Prolagus* of the late Villányian of the Italian peninsula (Solava; Tuscany, Ol-

ivola FU; Rook & Masini 1990), were tentatively referred to *P. aff. sorbinii* (Angelone & Rook 2012). This specific attribution was mainly based on some mandibular features shared by *P. aff. sorbinii* and the Solava specimen, which lacks species-diagnostic teeth.

The genus *Lagomys* was mentioned by Falconer (1868) among the vertebrates of Upper Valdarno (Tuscany). Its presence was eventually confirmed by Major in Stoppani (1873). However, *Lagomys* was not reported in subsequent faunal lists (Major 1875, 1876, 1884). Due to the lack of descriptions, figures, and references to repositories and to inventory numbers, it is not possible to know if such specimens were lost, or if their taxonomic assignment was later reconsidered. Indeed, in the lists of vertebrates of the Upper Valdarno reported by Major (1875, 1876, 1884), *Lagomys* was substituted with

Lepus Linnaeus, 1758 (see also next paragraph). Two more specimens of *Lagomys* from Upper Valdarno were described by Bosco (1899a, 1899b). Tobien (1935) argued that those specimens had to be ascribed to the genus *Prolagus*. Those specimens were not figured in any of the cited papers, and they are probably lost (Angelone & Rook 2012). It is impossible to guess neither their biochronological position (i.e. whether they can be assigned to the late Villányian Olivola FU, or to the early Biharian Tasso FU), or their specific (or even generic) attribution.

Oryctolagus Lilljeborg, 1873

The presence of a leporid in the Upper Valdarno was known since the late XIX century. In the oldest publications, faunal lists reported the presence of *Lepus* sp. (Major 1875, 1876, 1884). It must be remarked, though, that in previous publications the faunal lists of Upper Valdarno reported *Lagomys*, not *Lepus* (see previous paragraph). Eventually, Weithofer (1889) erected the species *Lepus valdarnensis* Weithofer, 1889 to include such materials. Bosco (1899a, 1899b) split the leporid from Upper Valdarno in two taxa (*L. valdarnensis* and *L. etruscus* Bosco, 1899), leaving undetermined postcranial remains in open nomenclature (*Lepus* sp.). On the other hand, Major (1899) reputed that the leporid material from Upper Valdarno pertained in its entirety to the Asian genus *Caprolagus* Blyth, 1845. Decades later, Viret (1954) assigned the same material to *Oryctolagus lacosti* (Pomel, 1853). An unsuccessful effort of revalidation of *L. valdarnensis* was attempted by Forteleoni (1971). Angelone and Rook (2012), agreeing with Viret (1954), considered the Upper Valdarno leporid remains as pertaining to the genus *Oryctolagus*. They validated and redescribed the species *O. valdarnensis* (Weithofer, 1889) (Fig. 2.d), including as a synonym *L. etruscus* (Angelone & Rook 2012). Indeed, the very large teeth and the presence of several “leporine” characters in the maxilla of *O. valdarnensis* (see Angelone & Rook 2012: 138) may be misleading, and explain its eventful taxonomic history.

Montagnola Senese records the oldest Italian *Oryctolagus*. The remains from Montagnola Senese were originally assigned to *Oryctolagus cuniculus* (Linnaeus, 1758) (Fondi 1972). Eventually, they were ascribed to *O. valdarnensis*, as well as the other late Villányian remains of *Oryctolagus* of central Italy,

namely those from Torre di Picchio, Casa Sgherri (Tuscany; Marcolini et al. 2000), and Upper Valdarno localities of Olivola FU (Angelone & Rook 2012 and references therein). The morphological differences noticed among the populations of *O. valdarnensis* recognized in the Italian peninsula are due to different factors: some changes may be related to temporal trends, others to geographical trends probably linked to ecological factors (Angelone & Rook 2012: 142).

Oryctolagus appears in Italy much later than the European first appearance of the genus (~3.5 Ma) and slightly after the first appearance of *O. lacosti*, a species with western-central European distribution, which is dated at ~2.5 Ma (López Martínez 2008; Angelone & Rook 2012). We exclude the presence of *O. lacosti* in the Italian peninsula during the late Villányian (contra Pelletier et al. 2015: fig. 1.E). In fact, in our opinion, all the late Villányian *Oryctolagus* remains up to now collected in Italy belong to *O. valdarnensis*.

Leporidae indet.

Faunal lists in Biddittu et al. (1979) and Casoli and Segre Naldini (1984) report the presence of *Lepus* sp. in the Fontana Acetosa fossiliferous locality (Anagni, Latium) dated to the latest Villányian or the to earliest Biharian basing on a controversial report of *Hippopotamus* (see Bellucci et al. 2014). Segre Naldini et al. (2009), probably basing on the same material taken into account by Biddittu et al. (1979), mention instead the presence of “*Oryctolagus* cf. *O. etruscus*”. Such material was not described nor figured.

As at the present state of the art all the leporids of the Villányian of central Italy have been ascribed to *O. valdarnensis*, it is quite likely that the leporid from Acqua Acetosa may be referred to this species.

Biharian (Early Pleistocene-early Middle Pleistocene)

Prolagus

A time span of ~1.4 Ma separate the early Villányian *P. aff. sorbinii* from Arcille and the conspecific remains found at Case Inferno (Tuscany, Tasso FU; Rook & Masini 1990; Angelone & Rook 2012). Such discontinuity does not represent the actual absence of *Prolagus* in central Italy, but is due to the poor Italian Pliocene record of fossil locali-

ties bearing continental vertebrates. A fragment of maxilla of *Prolagus*, discovered in a fissure infilling of uncertain age in Colleferro (Latium), shows morphological characters of P4-M2 compatible with *P. aff. sorbinii*, but a size comparable to *P. italicus* (CA and TK, unpublished data).

Remains of *Prolagus* have been reported also from Monte Riccio (Latium, Tasso FU; Mazzini et al. 2000), but they consist in fragmentary specimens, non-diagnostic at the species level. The Tasso FU records the latest reports of the genus *Prolagus* in the Italian peninsula.

Hypolagus

In the earliest Biharian, *Hypolagus* appears again in northern Italy, this time in the eastern Alpine region (Monte La Mesa, Veneto, Tasso FU; Marchetti et al. 2000) (Fig. 2.e). The dental morphodynamic indexes and the comparison with other European populations of *Hypolagus*, indicate that the sample from Monte La Mesa, formerly attributed by Marchetti et al. (2000) to *Hypolagus beremendensis* (Petényi, 1864), fits in the lower range of European populations of *Hypolagus brachygnathus* (Kormos, 1930) (Angelone 2013: fig. 3; see Čermák 2009 for nomenclatorial details about the genus *Hypolagus*). Indeed, the temporal and geographical distribution of *H. brachygnathus* (see Čermák 2009) support the taxonomic assignment of the remains from Monte La Mesa based on the tooth morphology.

Another early Biharian report of *Hypolagus*, slightly younger than the one from Monte La Mesa, is *H. aff. brachygnathus* from Pirro Nord (Apulia, Pirro FU; Angelone 2013) (Fig. 2.f). Unfortunately, the most recent revision of *Hypolagus* from Pirro Nord revealed that a large part of the material collected in the oldest surveys may be lost (Angelone 2013). Nevertheless, the remains available up to date, coupled with older literature data, were sufficient to make some interesting considerations. *Hypolagus* from Pirro Nord differs from the coeval central European *H. brachygnathus* by having higher dental morphodynamic indexes, coupled with a smaller dental size and a poor cursorial structure of the limbs (Fladerer & Fiore 2003; Angelone 2013). Such mix of advanced and primitive characters observed in *H. aff. brachygnathus* was explained hypothesizing the existence of an endemic, conservative Italian lineage of *Hypolagus* derived from a basal stock of *H. brachygnathus* of central Europe.

Oryctolagus

During the Biharian, *O. valdarnensis* is still present in Tuscany, Umbria, and Apulia (Casa Frata and other Upper Valdarno localities of Tasso FU; Pietrafitta and Monte Argentario, Farneta FU; and Pirro Nord, Pirro FU) (Borselli et al. 1980; Argenti & Kotsakis 2009; Angelone & Rook 2012 and references therein; Rook & Angelone 2013; Siori et al. 2014). It is worth to mention that in a younger paper, *Oryctolagus* from Pirro Nord is still reported as *O. aff. lacosti* (Angelone 2013). This is not due to a subsequent reconsideration of the taxonomic attribution of the taxon, but to simply to a long delay (2008–2013) between the manuscript approval and the publication of the paper and the impossibility to modify the text according to the new highlights occurred in between (see foreword in Angelone 2013: 96).

Oryctolagus sp. from the upper levels of Monte Peglia (latest early Biharian, Colle Curti FU) (Fig. 2.g) was originally classified as *Lepus* sp. (Van der Meulen 1973). Angelone and Rook (2012) and Angelone (2013), basing on a lower third pre-molar figured in Van der Meulen (1973: fig. 9), agree with López Martínez (1989), who reconsidered the taxonomical position of the specimen ascribing it to the genus *Oryctolagus*. Indeed, the measurements and the morphological features observable in Van der Meulen (1973), fit with their attribution to *O. valdarnensis*. However, the current unavailability of the specimens curated at the IsIPU, prevents well-founded taxonomic statements.

Oryctolagus sp. from Monte Peglia represents the last report of the older stock of Italian populations of *Oryctolagus* defined as Older *Oryctolagus* Populations in Angelone (2013). During the late Biharian there is no report of *Oryctolagus* in the Italian Peninsula.

In the first alluvial unit of Castagnone (Piedmont, Colle Curti FU), it was reported a leporid classified as *Oryctolagus* cf. *lacosti* (Giraudi et al. 2003). The same remains have been classified as Leporidae indet. by Siori and Sala (2007).

Caloi and Palombo (1994) reported fragmentary cranial remains of a leporid from the lacustrine sediments of Capena (Latium), and assigned them to *Lepus etruscus* (synonym of *Oryctolagus valdarnensis* according to Angelone & Rook 2012). The fossiliferous site of Capena was previously assigned to Pirro FU (Gliozzi et al. 1997), and eventually to an

age range between Pirro and Slivia FUs (Marra et al. 2018). The specimens were not figured, and were eventually lost.

Lepus Linnaeus, 1758

The oldest reliable record of the genus *Lepus* in the Italian peninsula occurs in the lower levels of Monte Peglia (late early Biharian, Colle Curti FU). The remains were ascribed to *Lepus terraerubrae* Kretzoi, 1956 (now *nomen dubium*, pers. comm. S. Čermák 2019) in the first and only paper dealing with the lagomorphs from Monte Peglia (Van der Meulen 1973) (Fig. 2.h). As well as *Oryctolagus* sp. from the upper levels of the same locality, this fossil hare is currently unavailable for updated comparisons.

Italian reports of *Lepus* older than the above mentioned one are probably the result of an error in the generic attribution. This may be the case, for example, of *Lepus* sp. from Soave Cava Sud (Veneto, late early Biharian, Pirro FU) mentioned in a nomenclatorial update (not a taxonomic revision) of old faunal lists of Plio-Pleistocene assemblages of NE Italy (Bon et al. 1991 and references therein).

Leporidae indet.

Ambrosetti et al. (1979) reported *Lepus euro-paens* Pallas, 1778 from Slivia (Friuli-Venezia-Giulia, late Biharian, Slivia FU), but such attribution was made only on a dimensional basis. Bon et al. (1992) revised the faunal assemblage from Slivia, but did not include the leporid. Thus, for the moment, it is preferable to leave such remains in open nomenclature as Leporidae indet.

A few remains of an undetermined leporid have been reported from San Lorenzo (Basilicata, latest Biharian, Ponte Galeria FU; Masini et al. 2005).

Toringian (late Middle Pleistocene-Late Pleistocene)

Ochotona Link, 1795

Fossil lagomorphs collected in the middle/upper levels of Visogliano A (Veneto; early Toringian, Isernia FU/Fontana Ranuccio FU) were at first attributed to *Ochotona* sp. (Bartolomei et al. 1977; Bartolomei & Tozzi 1978), and eventually classified as *Ochotona pusilla* (Pallas, 1769) by Abbazzi et al. (2000).

In the late Toringian, *Ochotona* cf. *pusilla* is reported in the lower levels of Tagliente Shelter (Vene-

to; Bartolomei et al. 1982; Sala 1990; Bon et al. 1991).

Oryctolagus

The genus *Oryctolagus* is absent in the Italian fossil record during the late Biharian (Slivia FU and Ponte Galeria FU). *Oryctolagus* reappears in the earliest Toringian (Borgio Verezzi, Liguria, Isernia FU; Nocchi & Sala 1997a, 1997b) with a new species, *O. burgi* Nocchi & Sala, 1997 (Fig. 2.i). *Oryctolagus* cf. *burgi* may be present also at Ponte Galeria 3 (Latium, Isernia FU; Kotsakis & Barisone 2008, and currently under revision by Sardella and colleagues). This species is unknown at present in the rest of Europe, and in Italy it is the oldest of the Modern *Oryctolagus* Populations, a stock of Italian *Oryctolagus* characterized by morphological features similar to extant species (Angelone 2013). At the present state of the art, *O. burgi* seems to be exclusive of the Isernia FU. The phylogenetic relationships of *O. burgi* with congeneric species is still a matter of debate (Nocchi & Sala 1997a, 1997b).

A large leporid found at Isernia (Molise, earliest Toringian, Isernia FU) was formerly reported as *Lepus* sp. (Sala 1983). Eventually, its taxonomic position was reconsidered as cf. *Oryctolagus* sp. (Sala 1996). In correspondence of the Fontana Ranuccio FU, *Oryctolagus* disappears again in the Italian fossil record.

In the Italian peninsula, the oldest report of *Oryctolagus cuniculus* (Fig. 2.j) occur in correspondence of the lower levels of Torre in Pietra (Latium, late early Toringian, Torre in Pietra FU; Caloi & Palombo 1978). Since late Toringian on, *O. cuniculus* becomes quite common in the Italian peninsula. Some early Toringian findings do not have a specific attribution and are reported in literature as *Oryctolagus* sp. (Tab. 1).

Callou (2003) argues that *Oryctolagus* may be absent from the Late Pleistocene and Early Holocene fossiliferous sites of southern France. We checked this possibility in the Italian fossil record: *Oryctolagus* is present in several localities of southern Italy assigned to MIS 5 and MIS 3 (see Tab .1, and López Martínez 2008: fig. 10), and in the MIS 4 of Arma delle Manie (Liguria; El Guennouni 2001). Thus, there is evidence of the survival of *Oryctolagus* in peninsular Italy in the Late Pleistocene at least until MIS 3. Anyway, the presence of *Oryctolagus* in southernmost Italy during the Last Glacial Maximum and the early Holocene can be inferred also

by indirect evidences, and a recent report suggests the survival of the wild rabbit in peninsular Italy also in the early Holocene (see below).

Lepus

Toringian Italian fossil remains of *Lepus* need a complete revision. The specifically determined remains are attributed to four extant species: *Lepus europaeus*, *Lepus corsicanus* De Winton, 1898 (Fig. 2.k), *Lepus timidus* Linnaeus, 1758, *Lepus capensis* Linnaeus, 1758. However, such specific determinations are often based on non-diagnostic remains, on dimensional features only, or rely on the known (or better said: supposed) biochronological and geographical Toringian distribution of the above mentioned extant species, which in its turn needs to be thoroughly revised, generating a dangerous circular reasoning. For this reason, pending a taxonomic revision of Italian fossil *Lepus*, we prefer to list in open nomenclature (*Lepus* sp.) several Toringian reports previously classified to the species level (see Tab. 1). They go to enlarge the list of Italian Toringian reports of *Lepus* which currently lack a determination at the species level (see Tab. 1, and Kotsakis et al. 2003 and references therein).

At present, *Lepus corsicanus* from the lower levels of Visogliano A (late Galerian, Isernia FU/Fontana Ranuccio FU; Abbazzi et al. 2000; Vismara 2012) represent the oldest reliable record of the species, followed by *L. cf. corsicanus* from Cretone (Latium, Fontana Ranuccio FU; Di Canzio et al. 2003).

The oldest reliable Italian reports of *L. europaeus* seems to date back to the late Toringian. Nevertheless, the remains of *L. europaeus* from central and southern Italy may pertain to *L. corsicanus* (cfr. Kotsakis 2008). Remains from tardiglacial assemblages of Calabria, classified as *L. europaeus*, have been eventually attributed to *Lepus* sp. (Mangano 2007; Marra 2009 both with references).

The endemic Italian hare, *L. corsicanus*, considered as a subspecies of *L. europaeus* by Miller (1912), was eventually revalidated on the basis of dental and cranial characters by Palacios (1996). Several authors refer to *L. corsicanus* the remains from Late Pleistocene fossiliferous sites of southern-central and southern Italy (see Tab. 1).

In northern and northern-central Italy, late Toringian remains of *Lepus* are frequently referred

to the mountain hare *Lepus timidus* (or, in older literature, to its synonym *Lepus variabilis* Pallas, 1778). In some cases, *L. timidus* is reported together with *L. europaeus*. *Lepus timidus* is a species associated to colder climates, so it is noteworthy its report at Grotte delle Striare (in the largest cave, lev. h, Apulia; Di Stefano et al. 1992), which represents the southernmost record in the Italian peninsula. Additional reports of *L. timidus* are listed in Capasso Barbato et al. (1991). Minieri et al. (1995 with references) lists 11 Toringian sites with *L. timidus*, 41 reports of *L. europaeus* (including *L. corsicanus*), and 19 fossiliferous sites with *O. cuniculus* (19). Most of the reports in Capasso Barbato et al. (1991) and Minieri et al. (1995) need a reassessment and are not listed in Tab. 1.

Several remains of leporids attributed by Pasa (1947) and Bartolomei (1964) to *Lepus mediterraneus* Wagner, 1841 and *L. europaeus* were collected from a few localities of NE Italy (Cengelle 1, Castello, Viatelle, Spessa II; late Biharian or Toringian after Bon et al. 1991 with references). Also for these remains is absolutely necessary a systematic revision.

Holocene

Oryctolagus

The presence of the genus *Oryctolagus* in the early Holocene was reported in old faunal lists, but such material was not figured and needs a restatement. *Oryctolagus* was introduced in Italy by humans for hunting and as livestock in the late Holocene (Angelici et al. 2008; Masseti 2008). After Rustioni et al. (2007), the rabbit is present in the late Neolithic (VI millennium BP) of Offida (Marches). However, it is quite likely that the rabbit found in southernmost Italy at Grotta di Latronico 3 (Basilicata, ~8000-7400 ky; Dini et al. 2008) may be not a human introduction, but a relict population.

Lepus

At the beginning of the Holocene, *L. europaeus* can be considered the predominant species of the genus in northern and central Italy, whereas *L. corsicanus* was probably distributed in southern-central and southern Italy (Angelici et al. 2008). It is worth to mention that, although its name may suggest an origin from Corsica, the species *L. corsicanus* is not autochthonous of Corsica. In fact, it has been introduced there by humans

	Age	Locality	Region	Species	References
early-middle Turolian	MN11	Baccinello V0	Tuscany	<i>Paludotona aff. minor</i>	Cirilli et al. 2016; Angelone et al. 2017
	?latest MN11-early MN12	Baccinello V1	Tuscany	<i>Paludotona etruria</i>	Dawson 1959; Hürzeler & Engesser 1976; Angelone et al. 2017
	late MN12-early MN13	Baccinello V2	Tuscany	<i>Paludotona minor</i>	Angelone et al. 2017
late Turolian	pre-evaporitic Messinian, MN13	Capo di Fiume	Abruzzi	<i>Prolagus cf. apricenicus</i>	Mazza et al. 1995; Angelone 2007
	MN13	Gargano (several fissure infillings)	Apulia	<i>Prolagus apricenicus</i>	Masini et al. 2013; Moncunill-Solé et al. 2016a
	MN13/?MN14	Gargano (several fissure infillings)	Apulia	<i>Prolagus apricenicus, Prolagus imperialis</i>	Mazza 1986a, 1986b, 1987; Mazza & Zafonte 1987; Angelone 2007; Masini et al. 2013; Moncunill-Solé et al. 2016a
	pre-evaporitic Messinian, MN13	Velona	Tuscany	<i>Prolagus cf. sorbinii</i>	Rook & Ghetti 1997; Ghetti et al. 2002; Angelone 2007; Angelone & Rook 2012
	pre-evaporitic Messinian, MN13	Baccinello V3	Tuscany	? <i>Prolagus sp., Alilepus meini</i>	Rook & Masini 1990; Angelone & Rook 2011, 2012
	evaporitic Messinian, MN13	Monte Castellaro	Emilia-Romagna	<i>Prolagus sorbinii</i>	Masini 1989
	post-evaporitic Messinian, MN13	Ciabòt Cagna	Piedmont	<i>Prolagus sorbinii</i>	Cavallo et al. 1993 as <i>Prolagus michauxi</i> ; Angelone & Cavallo 2010
	post-evaporitic Messinian, MN13	Moncucco	Piedmont	<i>Prolagus sorbinii, Leporidae indet.</i>	Angelone et al. 2011; Colombero et al. 2017
	post-evaporitic Messinian, MN13	Verduno	Piedmont	<i>Prolagus sorbinii</i>	Colombero et al. 2014
	post-evaporitic Messinian, MN13	Brisighella	Romagna	<i>Prolagus sorbinii, Trischizolagus sp.</i>	De Giuli 1989 as <i>Prolagus cf. sorbinii</i> and <i>Trischizolagus cf. maritsae</i> ; Masini 1989; Angelone 2007; Rook et al. 2015 with references
	post-evaporitic Messinian, MN13	[Casino]	Tuscany	[<i>Prolagus elsanus</i>]	Major 1875, 1899, 1905; Rüttemeyer 1876; López Martínez & Thaler 1975; Azzaroli et al. 1986; Angelone & Rook 2012 with references
	post-evaporitic Messinian, MN13	Cava Stingeti	Molise	<i>Prolagus sp., Leporidae indet.</i>	Cosentino et al. 2018
	latest Messinian	Borro Strolla lower synthem (=Cava Sefi)	Tuscany	<i>Trischizolagus sp.</i>	Abbazzi et al. 2008b; Angelone & Rook 2012
Ruscinian-early Villányian	earliest MN14	Borro Strolla upper synthem (=Cava Sefi)	Tuscany	<i>Prolagus cf. sorbinii</i>	Abbazzi et al. 2008b; Angelone & Rook 2012
	MN16a, Triversa FU	Arcille	Tuscany	<i>Prolagus aff. sorbinii</i>	Hürzeler & Engesser 1976; Angelone & Rook 2012
	MN16a, Triversa FU	Arondelli	Piedmont	<i>Prolagus savagei, Hypolagus petenyii</i>	Berzi 1967; Berzi et al. 1970; Azzaroli et al. 1986; Čermák 2009; Angelone & Rook 2012 with references
late Villányian	MN17, Coste S. Giacomo FU	Montagnola Senese (=Rosia)	Tuscany	<i>Prolagus italicus, Oryctolagus valdarnensis</i>	Fondi 1970, 1972; Azzaroli et al. 1986; Angelone 2008a, 2013; Angelone & Rook 2012
	MN17, Coste S. Giacomo FU	Coste S. Giacomo	Latium	<i>Prolagus italicus</i>	Bona et al. 2015
	MN17, Olivola FU	Torre di Picchio	Umbria	<i>Prolagus italicus, Oryctolagus valdarnensis</i>	Girotti et al. 2003; Angelone 2008a, 2013; Angelone & Rook 2012
	MN17, Olivola FU	Casa Sgherri	Tuscany	<i>Oryctolagus valdarnensis</i>	Marcolini et al. 2000; Angelone & Rook 2012; Angelone 2013
	MN17, Olivola FU	Solava	Tuscany	<i>Prolagus aff. sorbinii</i>	Angelone & Rook 2012 with references; Rook & Angelone 2013
	MN17, Olivola FU	Upper Valdarno (several localities)	Tuscany	<i>Oryctolagus valdarnensis</i>	Angelone & Rook 2012 with references; Rook & Angelone 2013
	latest Villányian/earliest Biharian	Fontana Acetosa	Latium	? <i>Oryctolagus valdarnensis</i>	Biddittu et al. 1979, Cassoli & Segre Naldini 1984; Segre Naldini et al. 2009; alternatively reported as <i>Oryctolagus cf. O. etruscus</i> or <i>Lepus sp.</i>
Biharian	Tasso FU/Olivola FU	[Upper Valdarno (several localities)]	Tuscany	[?Prolagus]	Angelone & Rook 2012 with references
	Tasso FU	Case Inferno	Tuscany	<i>Prolagus aff. sorbinii</i>	Rook & Masini 1990; Angelone & Rook 2012
	Tasso FU	Casa Frata	Tuscany	<i>Oryctolagus valdarnensis</i>	Borselli et al. 1980; De Giuli & Masini 1986
	Tasso FU	Upper Valdarno (several localities)	Tuscany	<i>Oryctolagus valdarnensis</i>	Angelone & Rook 2012
	Tasso FU	Monte Riccio	Latium	<i>Prolagus sp.</i>	Mazzini et al. 2000
	Tasso FU	Monte La Mesa	Veneto	<i>Hypolagus brachygnathus</i>	Marchetti et al. 2000; Angelone 2013
	?Early Pleistocene	Colleferro	Latium	<i>Prolagus sp.</i>	CA and TK unpublished data
	Farneta FU	Pietrafitta	Umbria	<i>Oryctolagus valdarnensis</i>	Argenti & Kotsakis 2009; Angelone & Rook 2012; Angelone 2013
	Farneta FU	Monte Argentario	Tuscany	<i>Oryctolagus valdarnensis</i>	Angelone & Rook 2012; Siori et al. 2014
	Pirro FU	Pirro Nord	Apulia	<i>Hypolagus aff. brachygnathus, Oryctolagus valdarnensis</i>	Fladerer & Fiore 2003; Angelone & Rook 2012; Angelone 2013
	Pirro FU	Soave Cava Sud	Veneto	? <i>Lepus sp.</i>	Bon et al. 1991
	Colle Curti FU	Castagnone	Piedmont	Leporidae indet.	Giraudi et al. 2003 as <i>Oryctolagus cf. lacostii</i> ; Siori & Sala 2007
	Colle Curti FU	Monte Peglia lower levels	Umbria	<i>Lepus terraerubrae</i>	Van der Meulen 1973; López Martínez 1989
	Colle Curti FU	Monte Peglia upper levels	Umbria	<i>Oryctolagus sp.</i>	Van der Meulen 1973; López Martínez 1989; Angelone 2013
	Colle Curti FU	[Capena]	Latium	? <i>Oryctolagus valdarnensis</i>	Caloi & Palombo 1994 as [<i>Lepus etruscus</i>]
	Silvia FU	Silvia	Venezia Giulia	Leporidae indet.	Ambrosetti et al. 1979 as <i>Lepus europaeus</i>
	Ponte Galeria FU	San Lorenzo	Basilicata	Leporidae indet.	Masini et al. 2005
early Toringian	Isernia FU	Isernia	Molise	cf. <i>Oryctolagus sp.</i>	Sala 1983 as <i>Lepus sp.</i> ; Sala 1996
	Isernia FU	Borgio Verezzi lower level (=Valdemino)	Liguria	<i>Oryctolagus burgi</i>	Nocchi & Sala 1997a, b
	Isernia FU	Ponte Galeria 3 (=Casal Selce)	Latium	<i>Oryctolagus cf. burgi, Lepus sp.</i>	Kotsakis & Barisone 2008; Sardella and coll. under study
	Isernia FU	Spessa II	Veneto	<i>Lepus sp.</i>	Bon et al. 1991
	Isernia FU/Fontana Ranuccio FU	Visogliano A lower levels	Veneto	<i>Lepus corsicanus</i>	Abbazzi et al. 2000; Vismara 2012
	Isernia FU/Fontana Ranuccio FU	Visogliano A middle/upper levels	Veneto	<i>Ochotona pusilla</i>	Bartolomei et al. 1977; Bartolomei & Tozzi 1978 as <i>Ochotona sp.</i> ; Abbazzi et al. 2000
	Fontana Ranuccio FU	Fontana Ranuccio	Latium	<i>Lepus sp.</i>	Biddittu et al. 1979 as <i>Lepus cf. capensis</i>
	Fontana Ranuccio FU	Bristie I	Venezia Giulia	<i>Lepus sp.</i>	Lugli & Sala 2000 as <i>Lepus europaeus</i>
	Torre in Pietra FU	Castel di Guido	Latium	<i>Lepus sp.</i>	Sala & Barbi 1996 as <i>Lepus cf. europaeus</i>
	Torre in Pietra FU	Torre in Pietra, lower levels	Latium	<i>Oryctolagus cuniculus, Lepus sp.</i>	Caloi & Palombo, 1978; Caloi et al. 1998
	Torre in Pietra FU	Cretona	Latium	<i>Lepus cf. corsicanus</i>	Di Canzio et al. 2003
	?Torre in Pietra FU	Borgio Verezzi upper level	Liguria	<i>Lepus sp.</i>	Tozzi 1969 as <i>Lepus europaeus</i> and reported as found in lower levels; Nocchi & Sala 1997a
	"Vitinia FU"	Torre in Pietra, upper levels	Latium	<i>Oryctolagus cuniculus</i>	Caloi & Palombo 1978; Caloi et al. 1998
	?early or late Toringian	Grotta Maggiore di San Bernardino (level unknown)	Veneto	<i>Lepus sp.</i>	Bartolomei 1960; for the age: López-García et al. 2017
	late Toringian	Caverna degli Orsi	Venezia Giulia	<i>Lepus europaeus, Lepus timidus</i>	Bon et al. 1991 with references; Berto & Rubinato 2013
Caverna Pocala		Venezia Giulia	<i>Lepus europaeus, Lepus cf. timidus</i>	Fabiani 1919, Bon et al. 1991 with references	
?late Toringian		Montorio	Veneto	<i>Lepus europaeus</i>	Pasa 1952; Bon et al. 1991
		Tagliente Shelter lower levels	Veneto	<i>Ochotona cf. pusilla</i>	Bartolomei et al. 1982; Sala 1990; Bon et al. 1991
		Tagliente Shelter upper levels	Veneto	<i>Lepus europaeus, Lepus cf. timidus</i>	Capuzzi & Sala 1980; Bon et al. 1991
		Grotta del Broion	Veneto	<i>Lepus europaeus</i>	Sala 1980; Bon et al. 1991
	Mezzena Shelter	Veneto	<i>Lepus europaeus</i>	Bartolomei et al. 1980; Bon et al. 1991	

Tab. 1 - List of lagomorph-bearing localities of continental Italy detailed with geographical location. See next page for caption.

Age	Locality	Region	Species	References	
	Grotta inferiore dei Covoli di Velo	Veneto	<i>Lepus europaeus</i>	Bona et al. 2007	
	Grotta della Volpe	Veneto	<i>Lepus timidus</i>	Pasa 1950a; Bon et al. 1991	
	Grotta A del Ponte di Veja	Veneto	<i>Lepus cf. europaeus, Lepus sp.</i>	Pasa 1950b; Bon et al. 1991	
	Zandobbio	Lombardy	<i>Lepus cf. europaeus</i>	Vialli 1957	
	Caverna Generosa	Lombardy	<i>Lepus sp.</i>	Bona et al. 2009	
	Arma delle Manie	Liguria	<i>Oryctolagus cuniculus</i>	El Guennouni 2001	
	Grotta del Principe lower levels	Liguria	<i>Oryctolagus cuniculus</i>	Barral & Simone 1971	
	Arene Candide	Liguria	<i>Lepus europaeus, Lepus timidus</i>	Cassoli & Tagliacozzo 1994	
	Monte Croara	Emilia	<i>Lepus cf. timidus</i>	Pasini 1969	
	Grotta Parignana lev. B	Tuscany	<i>Lepus timidus</i>	Farina 2012, 2014	
	Manciano	Tuscany	<i>Lepus cf. europaeus</i>	Petronio et al. 2014	
	Grotta di Sant'Agostino	Latium	<i>Oryctolagus cuniculus, ?Lepus europaeus</i>	Tozzi 1970	
	Grotta Barbara	Latium	<i>Lepus europaeus</i>	Caloi & Palombo 1989	
	Cava Muraci	Latium	<i>Lepus sp.</i>	Gatta et al. 2019	
tardiglacial	Grotta Mora Cavorso (Jenne)	Latium	<i>Lepus corsicanus</i>	Salari et al. 2011	
tardiglacial	Riparo Salvini	Latium	<i>Lepus europaeus</i>	Tang & Kotsakis 2008	
	Grotta Cola	Abruzzi	<i>Lepus europaeus</i>	Di Canzio & Petronio 2001	
	Grotta Rutina	Abruzzi	<i>Lepus sp.</i>	Saccà 2016	
	Grotta di Scario level A	Campania	<i>Lepus europaeus</i>	Ronchitelli et al. 1998	
	Grotta di Castelcivita	Campania	<i>Lepus europaeus</i>	Cioni et al. 1979; Masini & Abbazzi 1997	
	San Sidero 3	Apulia	<i>Oryctolagus cuniculus</i>	De Giuli 1983	
	Melpignano	Apulia	<i>Oryctolagus cuniculus, Lepus europaeus</i>	Bologna et al. 1994	
	Cava Donno	Apulia	<i>Oryctolagus cuniculus, Lepus corsicanus</i>	Pandolfi et al. 2017	
	Avetrana	Apulia	<i>Oryctolagus cuniculus, Lepus corsicanus</i>	Pandolfi et al. 2013; Kotsakis et al. in press	
	Tana delle Iene	Apulia	<i>Lepus sp.</i>	Conti et al. 2012	
	Cava Spagnuolo	Apulia	<i>Oryctolagus cuniculus</i>	Mecozzi et al. 2018	
	Ingarano	Apulia	<i>Oryctolagus cuniculus, Lepus sp.</i>	Capasso Barbato et al. 1992; Petronio & Sardella 1998 as <i>L. europaeus</i> ; for the age: Bedetti & Pavia 2007	
	Sternatia	Apulia	<i>Oryctolagus cuniculus</i>	Rustioni et al. 1994	
	Cardamone	Apulia	<i>Oryctolagus cuniculus, Lepus europaeus</i>	Rustioni et al. 2003	
	Grotte delle Striare	Apulia	<i>Lepus timidus</i>	Di Stefano et al. 1992	
	Grotta Romanelli	Apulia	<i>Oryctolagus cuniculus, Lepus corsicanus</i>	Blanc 1920; Fiore 2003; Tagliacozzo 2003; Riga et al. 2003	
tardiglacial	Grotta Paglicci	Apulia	<i>Lepus corsicanus</i>	Vismara 2012	
transition late Toringian/Holocene	Grotta delle Mura	Apulia	<i>Lepus corsicanus</i>	Bon & Boscato 1993; Vismara 2012	
	Grotta di Torre Nave	Calabria	<i>Lepus sp.</i>	Bulgarelli 1972; Mangano 2007; Marra 2009	
tardiglacial	Grotta di Romito	Calabria	<i>Lepus sp.</i>	Boscato et al. 1998; Mangano 2007; Marra 2009	
Holocene	~8000-7400 y	Grotta di Latronico 3	Basilicata	<i>Oryctolagus cuniculus</i>	Dini et al. 2008

Tab. 1 - List of lagomorph-bearing localities of continental Italy detailed with geographical location, age, lagomorph content (=the latest taxonomic attribution of the considered taxa in case of discrepancies), and main related bibliographical references. For Late Pleistocene reports of *Lepus* and *Oryctolagus* are reported only some selected findings. The fossiliferous sites older than the late Toringian age are ordered, as far as possible, in a relative chronological order. The sites of late Toringian age (=Late Pleistocene) are instead grouped according to a geographical criterion (Italian regions). Material that has been lost, unavailable for study, doubtful reports, and obsolete namings are highlighted between square brackets [...]. In shaded light grey are highlighted fossil endemic insular domains now located in continental areas: Tusco-Sardinia PB in light grey; Abruzzi-Apulia PB in darker grey. Faunal Units after Gliozzi et al. (1997) and Petronio and Sardella (1999). Age of fossiliferous sites after Kotsakis et al. (2003), Masini and Sala (2007, 2011), Sala and Masini (2007).

shortly before the XVI century (Vigne 1992).

As for *L. timidus*, there are not sufficient data about its Italian distribution during the Holocene.

Sylvilagus Gray, 1867

The American (Palearctic and Nearctic) species *Sylvilagus floridanus* (J.A. Allen, 1890) has been introduced in Piedmont (NW Italy) in 1966 for hunting purposes. In Italy, contrarily to other western and central-western European countries in which it was also introduced, it became naturalized, and eventually expanded in both territory and number in the north-west of the Italian peninsula (Gallo et al. 2005 and references therein; Angelici & Spagnesi 2008). At present, *Sylvilagus* represents a pest for agriculture and is a biological competitor of *Lepus europaeus* (Gallo et al. 2005).

TAXONOMIC OVERVIEW OF FOSSIL LAGOMORPHS OF ITALIAN ISLANDS: SARDINIA

Prolagus

The oldest report of the genus *Prolagus* in Sardinia dates back to the earliest part of the Late Pliocene (*P. aff. figaro*, Capo Mannu D1; Angelone et al. 2015) (Fig. 1,j, k). Such remains are likely to be the “missing link” between the continental species *P. sorbinii* and *Prolagus figaro* López Martínez in López Martínez & Thaler, 1975, the oldest of the two Sardinian insular endemic species. Actually, *P. aff. figaro* shows the basic morphology of *P. sorbinii*, but also the incipient modifications typical of insular endemic *Prolagus* (see Angelone 2005), later fully developed in *P. figaro*. No other reports of *Prolagus* are known in Sardinia before the latest Pliocene/

earliest Pleistocene, age of the oldest reports of *P. figaro* in the Monte Tuttavista fissure infillings (Angelone et al. 2015). *Prolagus figaro* (Fig. 1.l) characterizes the Capo Figari/Orosei 1 subcomplex of the *Nesogoral* FC and the Orosei 2 subcomplex of the *Microtus (Tyrrhenicola)* FC (latest Pliocene/earliest Pleistocene to late Early Pleistocene).

Prolagus sardus (Wagner, 1829) (Fig. 1.m) characterizes instead the Sardinian Middle Pleistocene-Holocene (Angelone et al. 2008, 2015 and references therein). This species appears in the Dragonara FsC of the *Microtus (Tyrrhenicola)* FC, and is reported in almost all Pleistocene and Holocene fossiliferous sites of Sardinia. The Monte Tuttavista fissure infillings yield an impressive record of *P. sardus* of different ages. Among the best known Sardinian fossiliferous sites bearing *P. sardus*, we mention Monte San Giovanni, Grotta dei Fiori, Is Ozeris, Bonaria, Cava Sant'Elia, Su Concali, Bolotana, Tavolara (Tobien 1935; Comaschi Caria 1959, 1968; Gliozzi et al. 1984; Anfossi et al. 1996; Melis et al. 2013; Zoboli & Pillola 2016a, 2016b, 2017; Zoboli 2017). A special mention is deserved by Grotta del Campanaccio, a cave in which two articulated skeletons of *P. sardus* have been recovered (Zoboli & Caddeo 2016). *Prolagus sardus* has been reported also from several Sardinian archaeological sites (e.g. Grotta Corbeddu; Dawson 1969; Sondaar et al. 1984), and was the subject of a palaeopathological study of the postcranial bones (Zoboli et al. 2018).

The turnover *P. figaro*/*P. sardus* is not due to the dispersal of a new immigrant in the insular domain, but to the anagenetic replacement of the first species by the latter. The striking morphological and dimensional similarities of the juvenile specimens of the younger populations of *P. figaro* and the adult specimens of the older samples of *P. sardus* led Angelone et al. (2015) to hypothesize that *P. sardus* may have been the direct descendant of *P. figaro* through a neoteny phenomenon. It is worth to mention that López Martínez and Thaler (1975) report *P. figaro* together with *P. sardus* in the fissures of Capo Figari. However, the presence of both species in the old collections of Capo Figari is likely to be due to sampling bias or taphonomical mixing. The presence of both *P. figaro* and *P. sardus* in the same sample has been reported also from Monte Tuttavista infilling XIp, but it is explained by Angelone et al. (2008) arguing that the infilling of XIp lasted longer than other studied samples of Monte Tuttavista.

The species turnover at the onset of the Dragonara FsC (~0.8/0.7 Ma; inferred from Palombo 2009: fig 2) is the most remarkable among those recorded in the Quaternary of Sardinia (Abbazzi et al. 2004; Palombo 2009), and is probably related to the climatic changes occurred during the Mid-Pleistocene transition (Moncunill-Solé et al. 2016b). It is very interesting to notice that *Prolagus*, in countertrend to other Sardinian small mammal lineages, does not experience an abrupt dental size increase in correspondence of the turnover. In fact, in the oldest population of *P. sardus* can be observed a drastic reduction of the dental size (about 30%) relative to its ancestor *P. figaro* (Moncunill-Solé et al. 2016b). Such decrease is not coupled with a body mass decrease: conversely, the body mass increases throughout the lineage *P. figaro*-*P. sardus*.

Prolagus corsicanus Giebel, 1847, reported in Sardinia by Vaufray (1929), and in the neighbouring island of Tavolara by Piveteau (1961), is a synonym of *P. sardus* (see Major 1899).

Leporidae indet.

Fossil leporids were unknown in Sardinia before the discovery of the Monte Tuttavista karst complex (Rook et al. 2003). The oldest Sardinian leporid record (earliest Late Pliocene, ~3.6 Ma) consists of a sole, ill-preserved, non-diagnostic tooth from Capo Mannu D1 (Angelone et al. 2015), left in open nomenclature as Leporidae indet. (Fig. 2.l). Hypotheses about the origin of Leporidae indet. from Capo Mannu D1 and its relationships with other Sardinian leporids are illustrated below.

Sardolagus Angelone, Čermák, Moncunill-Solé, Quintana, Tuveri, Arca, & Kotsakis, 2018

Sardolagus obscurus Angelone, Čermák, Moncunill-Solé, Quintana, Tuveri, Arca, & Kotsakis, 2018 (Fig. 2.m) is an endemic insular leporid reported from several fissures infillings of the Monte Tuttavista karst complex referable to the Capo Figari/Orosei 1 and Orosei 2 faunal sub-complexes (Early Pleistocene, ~2.1/1.9-1.1 Ma) (Abbazzi et al. 2004; Angelone et al. 2018). It is quite likely that the Early Pleistocene species *S. obscurus* may be phylogenetically linked to Leporidae indet. from the earliest Late Pliocene of Capo Mannu D1. However, such a statement can not be fully supported at present due to the extreme scantiness and bad preservation state of the remains from Capo Mannu D1. The

mosaic of primitive and advanced morphological characters of *S. obscurus* (see differential diagnosis in Angelone et al. 2018: 510), and the consequent difficulty to unravel its phylogenetical affinities, were responsible for the choice of its specific name (Angelone et al. 2018). Its morphological similarity with *Oryctolagus* misleded in the preliminary analyses Angelone in Rook et al. (2003) and in Abbazzi et al. (2004), who classified the Sardinian leporid as *Oryctolagus* aff. *lacosti*. Erecting the new genus *Sardolagus* to include the leporid materials from Monte Tuttavista, Angelone et al. (2018) proposed two alternative hypotheses to explain the mix of archaic and modern morphological features resulting in an *Oryctolagus*-like appearance: (1) either a convergent evolution from an archaeolagine/leporine ancestor, or (2) a selective reversal morphocline from an *Oryctolagus*-like leporine. If *S. obscurus* is linked to Leporidae indet. from Capo Mannu D1, the first hypothesis is the one which better fits the fossil record.

Oryctolagus

Oryctolagus cuniculus was introduced by humans in Sardinia, perhaps in Roman times (Vigne 1992: fig. 2), but its presence is attested with certainty since the Middle Ages (Delussu 1996; Vigne 1999).

Lepus

The extant Sardinian hare was at first quoted by Rüster (1835, fide Wagner 1841: 439) as *L. timidus*?. Eventually, Wagner (1841) considered it as a separate species with the name of *Lepus mediterraneus*. Miller (1912) and Palacios (1998) regarded the Sardinian hare as an independent, endemic species. Other authors (see Ellerman & Morrison-Scott 1951; Mitchell-Jones et al. 1999) considered the Sardinian leporid as a subspecies of *L. capensis*, i.e. the taxon that, according to Petter (1959, 1961), includes almost all Old World hares. It is worth to mention a provisional assignment of the Sardinian hare as a subspecies of *Lepus granatensis* Rosenhauer, 1856 (Hoffmann 1993; Hoffmann & Smith 2005). In the latest revision of Italian extant mammals, Angelici and Spagnesi (2008 and references therein) considered the Sardinian hare as a subspecies of *L. capensis*. Genetic analyses seem to point out that the Sardinian hare constitutes a separate species (Pierpaoli et al. 1999; Alves et al. 2003). However, in both cited papers the Sardinian hare continues to be addressed as *L. capensis mediterraneus*. Other mo-

lecular studies, even considering the Sardinian hare as an independent species, refer to it as *Lepus* sp. (Suchentrunk et al. 2006; Scandura et al. 2007).

On a morphological basis, Palacios (1998) individuate the source of Sardinian hares in populations of the coastal region of northern Africa. Molecular data analyses (Scandura et al. 2007) suggest Tunisia as a potential source area for the introduction.

The earliest Sardinian reports of the hare occur during the Bronze Age (Nuraghe Santu Antine, ~4000-3000 years BP; Masala 2015), and during the Bronze/Iron Age (Santa Niedda, ~3000 years BP; Wilkens 2003, see also Wilkens & Delussu 2003).

TAXONOMIC OVERVIEW OF FOSSIL LAGOMORPHS OF ITALIAN ISLANDS: SICILY

Prolagus

De Gregorio (1925) mentions the presence of *Myolagus* Hensel, 1856 (= *Prolagus*) at Grotta della Castellana, a fossil assemblage attributed to the Spinagallo FC (=“*Elephas falconeri*” FC in Bonfiglio et al. 2002), or to the Maccagnone FC (=“*Elephas mnaidriensis*” FC in Bonfiglio et al. 2002). Indeed, the specimen figured in De Gregorio (1925: pl. 3, n. 33-34) has a size and an overall morphology comparable to *Prolagus*. However, the specimen is lost and the figures are not detailed enough to allow a confident generic attribution.

Hypolagus

A couple of upper jaws and a few teeth of a leporid were reported from Monte Pellegrino (Monte Pellegrino FC), and classified as *Lepus* sp. by De Gregorio (1886). Some decades later, the remains were assigned to *Lepus (Oryctolagus)* (De Gregorio 1925). Eventually, Thaler (1972) attributed the remains to the genus *Hypolagus*. Until 2002, subsequent publications reprised this taxonomic assignment (Bonfiglio et al. 2002 and references therein). A specific attribution was made by Fladerer and Fiore (2003), who erected the insular endemic taxon *Hypolagus peregrinus* Fladerer & Fiore 2003 (Fig. 2.n). Basing on the structure of the limbs, Fladerer and Fiore (2003) argue that *H. peregrinus* stemmed out from populations of the Early Pleistocene continental European species *H. brachygnathus* older than 1.2 Ma. Local conditions (insularity and a rocky,

steep environment) led to forelimb modifications resulting in the ambulatory locomotion that characterized *H. peregrinus* (Fladerer & Fiore 2003). As for the teeth structure, it is interesting to compare *H. peregrinus* to other Italian species. Whereas the dental morphodynamic indexes of *H. petenyii* from Arondelli and *H. brachygnathus* from Monte La Mesa fit into the cloud of the corresponding European populations, those of *H. aff. brachygnathus* from Pirro Nord and *H. peregrinus* clearly stand out, apparently forming a side branch (Angelone 2013: fig. 3). These observations suggest a close relationship between the peninsular endemic *H. aff. brachygnathus* from the late early Biharian of south-eastern Italy, but deserve further investigations.

Oryctolagus

The hypothesis commonly accepted by zoologists is that the introduction of rabbit in Sicily by humans probably occurred in Roman times (Flux 1994; Masseti & De Marinis 2008), but according to Lo Valvo et al. (2014) the oldest remains of *Oryctolagus* in the island date back to the Middle Ages. However, there are some reports of the presence of *O. cuniculus* in Sicily in more ancient times. Lagomorph remains recovered in the upper layer of the Grotta di San Teodoro were classified as *Lepus cuniculus* by Anca (1867). According to Mangano and Bonfiglio (1998), Grotta San Teodoro 2 is a level of tardiglacial age, but it is not to be excluded that part of the fossils collected in this layer may be reworked. Masini et al. (2008: fig. 4) report the appearance of *O. cuniculus* in Sicily during the transition from the Castello FC to the Holocene faunas. Villari (1986) reports remains of wild rabbits from Grotticella di Porto Palo and from Grotta Corruggi, both dated to the early post-glacial, and from the Basile Caves in strata of the early or middle Bronze Age. These evidences suggest that Sicily, as well as southernmost Italy and some Italian minor islands, represented a *refugium* for *O. cuniculus* during the Last Glacial Maximum and the earliest Holocene.

Lepus

The genus *Lepus* is reported in Sicily since the Late Pleistocene of Grotta del Castello (Regàlia 1907a), the type locality of the Castello FC (the most recent Sicilian FC), characterized by the absence of endemic elements (Bonfiglio & Kotsakis

1987; Bonfiglio et al. 2002). Those remains were originally attributed to *L. europaeus* (*ibid.*). All Late Pleistocene and Holocene leporids of Sicily require a systematic review, however, in our opinion it is extremely probable that the materials from Grotta del Castello may pertain to *L. corsicanus*, the species currently living throughout the island (Angelici & Spagnesi 2008).

Lepus has also been reported from the II Neolithic phase of Grotta dell'Uzzo (Holocene; Tagliacozzo 1993).

TAXONOMIC OVERVIEW OF FOSSIL LAGOMORPHS OF ITALIAN ISLANDS: MINOR ISLANDS

Fossil remains of lagomorphs have been discovered in some minor Italian islands. Most of the remains listed below date back to the first half of the XX century and need a taxonomic revision. All the faunal assemblages are balanced (mainland type *sensu* Dermitzakis & Sondaar 1978), and can be referred to the Toringian (see Tab. 2 for details). They reached the islands taking advantage of different low stands of the sea level occurred in correspondence of cold climatic phases.

In the Grotta dei Colombi, on the island of Palmaria (Liguria), Regàlia (1893, 1900) reported three species of leporids, namely *Lepus cuniculus*, *L. timidus*, and *L. variabilis* in a Late Pleistocene faunal assemblage. Cigna et al. (1967) assign to *L. europaeus* the fossils classified as *L. timidus* (or *L. variabilis*) by Regàlia (1893).

Del Campana (1910) reports from Grotta di Reale, in the Elba Island (Tuscany), two species of *Lepus*: *L. timidus* and *Lepus meridionalis* Génè in Gervais, 1859. The latter species is at present reputed *nomen nudum* and put in synonymy with *L. europaeus*. Mochi (1911) assigns all the remains of leporids from Grotta di Reale to *L. europaeus*.

On the island of Pianosa (Tuscan archipelago), De Stefano (1913) reports the presence of *L. timidus* together with the rodent *Marmota*. In more recent papers, the presence of *Marmota* has not been confirmed. Azzaroli (1978 with references) and Azzaroli et al. (1990) argue that the Pianosa fossils belong to two faunal assemblages of different age, both assigned to the Late Pleistocene. The one containing *Lepus* is the youngest.

Island	Age	Faunal complex	Locality	Species	References	
Sardinia	earliest Late Pliocene (7latest Pliocene-) Early Pleistocene	Capo Mannu D1 F5C	Capo Mannu D1 (=Mandriola)	<i>Prolagus aff. figaro</i> , Leporidae indet.	López Martínez & Thaler 1975; Angelone et al. 2015 with references	
		Capo Figari/Orosei 1 F5C	Monte Tuttavista (several karst infillings)	<i>Prolagus figaro</i> , <i>Sardolagus obscurus</i>	Rook et al. 2003; Abbazzi et al. 2004; Angelone et al. 2008; Moncunill-Solé et al. 2016b; Angelone et al. 2018	
	late Early Pleistocene	Orosei 2 F5C	Monte Tuttavista (several karst infillings)	<i>Prolagus figaro</i> , <i>Sardolagus obscurus</i>	Rook et al. 2003; Abbazzi et al. 2004; Moncunill-Solé et al. 2016b; Angelone et al. 2018	
	Middle Pleistocene-?Holocene		Dragonara F5C	Monte Tuttavista (several karst infillings)	<i>Prolagus sardus</i>	Rook et al. 2003; Abbazzi et al. 2004; Angelone et al. 2008; Moncunill-Solé et al. 2016b
			Dragonara F5C	Grotta dei Fiori	<i>Prolagus sardus</i>	Melis et al. 2013
			Dragonara F5C	Is Oreris	<i>Prolagus sardus</i>	Gliozzi et al. 1984
			Dragonara F5C	Monte San Giovanni	<i>Prolagus sardus</i>	Tobien 1935; Anfossi et al. 1996
			Dragonara F5C	Dragonara	<i>Prolagus sardus</i>	Tobien 1935
			Dragonara F5C	Su Concalli	<i>Prolagus sardus</i>	Zoboli & Pillola 2017
			Dragonara F5C	Bolotana	<i>Prolagus sardus</i>	Zoboli & Pillola 2016a
			Dragonara F5C	Grotta del Campanaccio	<i>Prolagus sardus</i>	Zoboli & Cadedeo 2016
			Dragonara F5C	Cava S. Elia	<i>Prolagus sardus</i>	Comaschi Caria 1959
			Dragonara F5C	Bonaria	<i>Prolagus sardus</i>	Zoboli & Pillola 2016b
	latest Pleistocene		Dragonara F5C	Grotta Corbeddu	<i>Prolagus sardus</i>	Dawson 1969; Sondaar et al. 1984
			Dragonara F5C	Tavolara	<i>Prolagus sardus</i>	Tobien 1935; Piveteau 1961; Anfossi et al. 1996
Holocene		Bronze Age	Nuraghe Santu Antine	<i>Prolagus sardus</i> , <i>Lepus mediterraneus</i>	Masala 2015	
Sicily	Early Pleistocene	Monte Pellegrino FC	Monte Pellegrino	<i>Hypolagus peregrinus</i>	De Gregorio 1886 as <i>Lepus</i> sp.; Thaler 1972; Fladerer & Fiore 2003	
	Early/Middle Pleistocene	Spinagallo FC or Maccagnone FC	Grotta della Castellana	?[<i>Prolagus</i>]	De Gregorio 1925 as <i>Myolagus</i>	
	Late Pleistocene	Castello FC	Grotta del Castello	<i>Lepus corsicanus</i>	Regàlia 1907a; Masini et al. 2008 with references as <i>L. europaeus</i>	
	latest Pleistocene	tardiglacial	Grotta San Teodoro 2	<i>Oryctolagus cuniculus</i>	Anca 1867 as <i>Lepus cuniculus</i> ; Mangano & Bonfiglio 1998	
	latest Pleistocene/Holocene	Castello FC/Holocene	-	<i>Oryctolagus cuniculus</i>	Masini et al. 2008 with references	
	Holocene	early post-glacial	Grotticella di Porto Palo and Grotta Corruggi	<i>Oryctolagus cuniculus</i>	Villari 1986	
	Holocene	II Neolithic phase	Grotta dell'Uzzo	<i>Lepus</i> sp.	Tagliacozzo 1993	
Palmaria	latest Pleistocene		Grotta dei Colombi	<i>Oryctolagus cuniculus</i> , <i>Lepus europaeus</i> , <i>Lepus timidus</i>	Regàlia 1893, 1900; Cigna et al. 1967	
Elba	latest Pleistocene		Grotta di Reale	<i>Lepus europaeus</i>	Del Campana 1910; Mochi 1911	
Pianosa	latest Pleistocene			<i>Lepus timidus</i>	De Stefano 1913; Azzaroli 1978 with references; Azzaroli et al. 1990	
Capri	late Middle Pleistocene		Quisisana-Certosa	<i>Oryctolagus cuniculus</i>	Capasso Barbato & Gliozzi, 1995	
	Holocene (2ky BP)*		Marina Grande	<i>Oryctolagus cuniculus</i>	Albarella, 1992; Masseti & De Marinis 2008	
Nisida	Holocene (2ky BP)*			<i>Oryctolagus cuniculus</i>	Barrett-Hamilton 1912	
San Domino (Tremi Islands)	"post-tyrrhenian"		Cala degli Inglesi and Grotta del Sale	<i>Oryctolagus cuniculus</i>	Pasa 1953	
Levanzo (Aegadian Islands)	latest Pleistocene (Mesolithic)	probably Castello FC	Grotta di Cala Genovesi	<i>Oryctolagus cuniculus</i>	Cassoli & Tagliacozzo 1982	
Pantelleria	Bronze Age*			?[<i>Oryctolagus cuniculus</i>]	Trocchi & Riga 1995; Masseti & De Marinis 2008 both citing Wilkens 1987 who, however, does not report the presence of this species in the text	

Tab. 2 - List of lagomorph-bearing localities of Italian islands detailed with age, lagomorph content (=the latest taxonomic attribution of the considered taxa in case of discrepancies), and main related bibliographical references. For Late Pleistocene Sardinian reports of *Prolagus* we list only some selected localities. Material that has been lost, unavailable for study, and doubtful reports/obsolete namings are highlighted between square brackets [...]. For the biochronology of continental Plio-Pleistocene fossiliferous sites of Sardinia, we follow the scheme proposed by Palombo (2006, 2009, 2018b) and Palombo and Rozzi (2014). For Sicily, we follow the scheme proposed by Kotsakis (1979), modified by Bonfiglio and Kotsakis (1987) and Bonfiglio et al. (2002). For minor islands we apply the biochronological schemes followed for mainland Italy (see Material and Methods and Tab. 1), and the listed reports are arranged in latitudinal order. *: introduced by humans.

In the Quisisana-Certosa fossil site, located in the island of Capri (Campania), and biochronologically dated to ~250-150 ky, Capasso Barbato and Gliozzi (1995) report the presence of the rabbit, *O. cuniculus*.

The rabbit is present in Capri also in archaeological deposits, introduced by humans in Roman age (~2 ky BP) (Albarella 1992; Masseti & De Marinis 2008 and references therein). In the neighbouring island of Nisida (Campania), Barrett-Hamilton (1912) reports the introduction of *O. cuniculus* during the Roman Imperial Age. The presence of *O. cuniculus*, introduced by humans, in an archaeological layer of Bronze Age in the Pantelleria Island (Sicily), was mentioned by Trocchi and Riga (2005) and Masseti and De Marinis (2008) purportedly basing on a former report (Wilkens 1987). However, Wilkens (1987) does not mention the rabbit among the studied remains.

Of particular interest are the following re-

ports of wild rabbits (=not introduced by humans) in some fossiliferous sites of Italian minor islands:

- Pasa (1953) reports the presence of *O. cuniculus* in the island of San Domino (Cala degli Inglesi and Grotta del Sale, Tremi Islands, Apulia), in coastal deposits of "post-tyrrhenian" age. If we consider the Tyrrhenian as a chronostratigraphic unit for the Late Pleistocene whose boundaries are at 130 ky and 11.5 ky (Cita et al. 2005), the *Oryctolagus*-bearing fossil sites of the Tremi Islands can be assigned to the Holocene. This attests to their arrival into the archipelago during the Last Glacial Maximum, an indirect evidence of their persistence in the Italian peninsula after MIS 3.

- Cassoli and Tagliacozzo (1982) mention *O. cuniculus* in the Grotta di Cala Genovesi, on the island of Levanzo (Aegadian Islands, Sicily). The fossil assemblage includes *Equus hydruntinus* Regàlia, 1907, a taxon characteristic of the Castello FC (Marra 2013 and references therein).

DISCUSSION AND CONCLUSIONS

Taxonomic and phylogenetic novelties

The principal novelties relative to Italian lagomorph taxonomy arisen in the last 15 years are the following:

- after several decades, *Paludotona*, the oldest known Italian lagomorph genus, known from the insular Turolian domain of the Tusco-Sardinia PB, ceased to be monospecific, due to the description of *P. minor* and *P. aff. minor* (Angelone et al. 2017), which join *Paludotona etruria* erected in the 50ties of the last century (Dawson 1959).

- For the first time Italy records stem lagomorphs. In fact, the features that led some authors to classify *Paludotona* as an ochotonid are instead the result of a convergent evolution (Angelone et al. 2017).

- The teeth morphology of *Paludotona* indicates that its continental ancestor should be sought among pre-MN2 European lagomorphs (Angelone et al. 2017). This phylogenetic datum provides a minimum age constraint to the onset of the Tusco-Sardinia PB to the earliest Miocene.

- Recent revisions confirmed the presence of *Prolagus* in BV3; the sole specimen from BV3, unfortunately not diagnostic at the species level, is among the oldest *Prolagus*-bearing localities of peninsular Italy.

- The presence of *Hypolagus* in BV3 was instead definitively discarded, as those remains were ascribed to the genus *Alilepus* (Angelone & Rook 2011).

- In older literature, Plio-Pleistocene *Prolagus* findings of the Italian peninsula did not have a clear specific attribution (as an example, see synonymic list of *P. aff. sorbinii* in Angelone & Rook 2012: 133-134). At the present state of the art, Plio-Pleistocene *Prolagus* of peninsular Italy are assigned to the species *P. savagei/P. aff. sorbinii* and to *P. italicus*.

- The taxonomic mayhem relative to the Valdarno leporid (*Oryctolagus valdarnensis*), known in literature since the XIX century, has been ended revalidating the species, and excluding any affinity with the genus *Lepus* (Angelone & Rook 2012 and references therein).

- *Prolagus aff. figaro*, *P. figaro*, and *P. sardus* have been recognized as forming an anagenetic lineage (Angelone et al. 2015). *Prolagus aff. figaro* is now reputed to be phylogenetically close to *P. sorbinii*,

and this means that the lineage originated from the Italian peninsula, and not from SW Europe as previously thought (López Martínez & Thaler 1975). Moreover, the fact that *P. sardus* has been recognized as a descendant of *P. figaro*, and not of *P. calpensis* (see López Martínez & Thaler 1975), eliminates the long-debated enigma relative to the age and modalities of its dispersal to Sardinia (Angelone et al. 2015).

- The discovery of leporids in the Late Pliocene and Early Pleistocene of Sardinia (*Sardolagus obscurus* and Leporidae indet.) is a quite important novelty, even if at present their phylogenetic affinities are unknown.

- The 8 new lagomorph species described, revalidated, or individuated without formalization in the last 15 years in the Italian territory are endemic. Several of them are endemic to the Italian peninsula (continental endemisms), whereas others are insular endemics. At present, Italy records 3 endemic species of stem lagomorphs (*Paludotona aff. minor*, *P. etruria*, and *P. minor*, all of them insular endemics); 9 species of ochotonids, of which 5 insular endemics (*Prolagus apricenicus*, *P. imperialis*, *P. aff. figaro*, *P. figaro*, *P. sardus*) and 2 continental endemics (*Prolagus italicus*, *P. savagei/P. aff. sorbinii*); and 14 species of leporids, of which 5 continental endemics (*Alilepus meini*, *Hypolagus aff. brachygnathus*, *Oryctolagus valdarnensis*, *O. burgi*, *Lepus corsicanus*) and 2 insular endemics (*Hypolagus peregrinus*, *Sardolagus obscurus*/Leporidae indet.); the status of *Trischizolagus* sp. must be verified.

Biochronology

The oldest lagomorphs recorded in the Italian territory are stem lagomorphs (*Paludotona* spp.), exclusive of the early-middle Turolian of the Tusco-Sardinia PB. Every species of *Paludotona* characterizes a precise time interval, corresponding to a local biochron (BV0, BV1, BV2). Nevertheless, the biochronological distribution of *Paludotona* is not limited to BV0-BV2 (~8.3-6.7 Ma). Its continental ancestor has to be sought among European species with hourglass-shaped lower third premolar, a morphology that disappeared in the fossil record after MN1-2 (Angelone et al. 2017). Thus, *Paludotona* possibly existed for ~12.6 Ma. *Paludotona*, which became extinct in the earliest Messinian, is the last of stem lagomorphs to survive. In fact, the last continental stem lagomorphs did not survive after the

early Late Miocene (~9 Ma; López Martínez 2008: figs 3, 5, 6). An endemic insular stem lagomorph, *Gymnesycolagus gelaberti* Mein & Adrover, 1982, persisted after the early Late Miocene in Western Mediterranean insular environments (Balearic Islands; Quintana & Agustí 2007 and references therein). However, it became extinct in the early Tortonian, earlier than *Paludotona*.

Ochotonids appear quite late in the Italian territory with respect to European mainland. In fact, *Prolagus*, abundant and widespread in Europe since the Early Miocene, reaches the Abruzzi-Apulia PB and the newly formed Italian peninsula only in the early Messinian. Even if morphological and palaeobiogeographical evidences point out that it must have arrived in the insular domain already in the earliest Messinian (Angelone 2007), the endemic insular *Prolagus apricenicus* is reported in the fossil record only in the latest Miocene-earliest Pliocene infillings of Gargano (Abruzzi-Apulia PB). The submergence of the Gargano Archipelago at the Mio/Pliocene boundary caused the extinction of the whole insular endemic assemblage of which *P. apricenicus* was part, including its possible sister species *P. imperialis*. Thus, it is possible to estimate that the species *P. apricenicus* lasted ~1.7-1.8 Ma, whereas we do not have enough information to estimate the time span lived by *P. imperialis*. In the territories which formed the Italian peninsula after its connection to European mainland, the oldest available fossil record of *Prolagus* (early Messinian) is roughly coincident with the time of its dispersal. *Prolagus* thrives in peninsular Italy for ~5Ma, until the early Biharian, and its absence in the Ruscianian fossil record of mainland Italy is probably due to the lack of data relative to continental Early Pliocene sediments in Italy.

Also leporids disperse to Italy during the Messinian. The first occurrence of leporid genera in Italy is always delayed with respect to continental Europe. The first genus to reach the Italian peninsula is *Alilepus*, followed by *Trischizolagus*. They do not last long: *Alilepus meini* is exclusive of the early Messinian of BV3 (~0.3 Ma), and *Trischizolagus* sp. probably lasts even less, as it is known only in the post-evaporitic Messinian of northern-central Italy.

Leporids re-appear in the Italian peninsula at ~3.2 Ma (early Villányian, Triversa FU; see Masini & Sala 2007) with *Hypolagus petenyii*. With this sole datum, it is impossible to make any inference about the temporal distribution of *H. petenyii* in Italy. *Hy-*

polagus disappears from the Italian fossil record for ~1.4 Ma. When it is recorded again, the new Italian species of *Hypolagus* are phylogenetically related to *H. brachygnathus*, but as in the case of *H. petenyii*, there is one sole report for every taxon: *Hypolagus brachygnathus* at ~1.8 Ma (earliest Biharian, Tasso FU), *H. aff. brachygnathus* at ~1.3-1.2 Ma (late early Biharian, Pirro FU), and *H. peregrinus* in correspondence of the Monte Pellegrino FC in Sicily. The terminal part of the Monte Pellegrino FC approximately corresponds to the late early Biharian (see Masini et al. 2008: fig. 5), with an upper limit at ~0.9 Ma or ~1 Ma (Masini et al. 2008; Marra 2013). Estimating the persistence of *H. peregrinus* in Sicily is more complicated. Masini et al. (2008: fig. 6) estimate it in ~0.7 Ma, which means a dispersal at ~1.8-1.7 Ma. According to Fladerer and Fiore (2003), the dispersal of the forerunner of *H. peregrinus* to the island occurred at ~1.3-1.2 Ma. We know that the earliest expansion of the distribution area of *H. brachygnathus* occur since the latest Villányian (see Čermák 2009), and that *H. peregrinus* and *H. aff. brachygnathus* from Pirro Nord are phylogenetically close and originated from a basal form of *H. brachygnathus* (Fladerer & Fiore 2003). Thus, the first hypothesis implies that one of the oldest dispersal waves of *H. brachygnathus* reached southern Italy and Sicily. The latter hypothesis implies instead a two-step model: *H. brachygnathus* dispersed to southern Italy first, and the dispersal to Sicily was delayed at ~1.3-1.2 Ma. A dispersal from Europe to southern Italy and Sicily at ~1.3-1.2 Ma fits too tight with the proposed phylogenetic setting which excludes from the ascendance of *H. peregrinus* and *H. aff. brachygnathus* from Pirro Nord the advanced forms of European *H. brachygnathus*, which appear at ~1.2 Ma.

As well as *Hypolagus*, also *Oryctolagus* dispersed several times into the Italian peninsula. The Italian endemic species *O. valdarnensis* appeared at ~2.1 Ma (MN17, late Villányian, Coste S. Giacomo FU), much later than the first appearance of the genus in Europe, and persisted until ~1.2 Ma (late early Biharian, Pirro FU). It is worth to notice that, in Pirro Nord, *O. valdarnensis* is reported in faunal lists together with *Hypolagus aff. brachygnathus*. However, the most recent review of the lagomorphs of Pirro Nord evidences that the two genera were never present in the same fissure (Angelone 2013). This datum may be of biochronological importance, but it has to be further investigated. *Oryctolagus* fossil

remains dated at ~1 Ma (latest early Biharian, Colle Curti FU) must be revised. At ~0.6 Ma, *Oryctolagus* re-appears in the Italian fossil record in the earliest phases of the early Toringian (Isernia FU) with *O. burgi*, another Italian endemic species not directly related to *O. valdarnensis*. The extant rabbit, *O. cuniculus*, appears in the Italian peninsula at ~0.3 Ma (late early Toringian, Torre in Pietra FU), delayed with respect to the first appearance of *O. cuniculus* in the Iberian peninsula (~0.6 Ma; López Martínez 2008). *Oryctolagus cuniculus* persists as a wild species in southernmost sectors of Italian mainland during the Last Glacial Maximum and during the Holocene (at least until ~8-7.4 ky). Sicily and Southern Italian islands (Tremiti Islands, Sicily, and the Aegadian Islands) host wild rabbits during the latest Pleistocene/early Holocene. This represents a very important biochronological and palaeobiogeographical datum, as the rabbit was thought to become extinct during the Last Glacial Maximum anywhere except for the Iberian peninsula.

Lepus appears much later with respect to *Oryctolagus* in the Italian peninsula (~1 Ma vs. ~2.1 Ma respectively), and with a noticeable delay with respect to continental Europe, where the oldest dispersals of *Lepus* occurs at ~2 Ma. The so-called *Lepus terraerubrae* from the lower levels of Monte Peglia (late early Biharian, Colle Curti FU) is the oldest reliable report of the genus *Lepus* in Italy (~1.0 Ma) or slightly earlier. The report of *Lepus* in the Slivia FU is not certain, in the Ponte Galeria FU there is only a report of an undetermined leporid, and in the Isernia FU there is no *Lepus* report. The extant species of *Lepus* appear in Italy between Isernia FU and Fontana Ranuccio FU. This means a discontinuity of ~0.6 Ma in the Italian record of *Lepus*. According to the available fossil record (which is pending a massive systematic revision, though), the oldest reliable report of the extant species of *Lepus* pertains to *L. corsicanus*, followed in the earliest late Toringian by *L. europaeus*, and by *L. timidus*. This latter species appears in Italy in correspondence of the MIS 2 (24-11.6 ky). In the Castello FC (late MIS 3/early MIS 2, ~25 ky), the genus *Lepus* appears for the first time in Sicily.

The Asian genus *Ochotona*, the sole extant survivor among the once flourishing family Ochotonidae, is reported twice in NE Italy. Those appearances are related to the expansion of the distribution area of *Ochotona* occurred in two different cold phases: MIS 12/MIS 10 (474-427 ky or 364-334 ky), and MIS 4 (74-59 ky). The importance of this datum, though,

is more palaeoecological/palaeoclimatical than biochronological.

Prolagus flourishes in Sardinia for ~3.6 Ma, i.e. since the earliest late Pliocene to historical epoch, but its record is not continuous. In fact, the Sardinian lagomorph record has a gap of at least ~1.5 Ma between Capo Mannu D1 and the older remains of *Prolagus* from Monte Tuttavista, dated at ~2.1/1.9 Ma. The minimum time span for the persistence of *P. figaro* is ~1.4 Ma, whereas *P. sardus* lasts ~0.8 Ma. The remains of *P. figaro* and *P. sardus* are so extremely abundant that it was possible to perform morphodimensional analyses of the populations that resulted in a preliminary relative chronological arrangement of the *Prolagus*-bearing fissure infillings of Monte Tuttavista (Angelone et al. 2008, 2009). The proposed order of the karst fissures containing *P. figaro* is, from older to younger: X3-IVm-X4-X5. For the infillings containing *P. sardus*, instead, the proposed order is, from older to younger: IV5-IV20-XIr-VIb6. These arrangements are in slight discordance with the relative chronological order of the infillings based on several other mammalian taxa of Monte Tuttavista proposed by Palombo (2009: fig. 2). Such results are quite encouraging because they demonstrate that lagomorphs can be used for biochronological purposes with a very high resolution (Angelone 2008b; Angelone et al. 2008, 2009). The biochronological history of leporids in Sardinia follow the same pattern of ochotonids, except that it is shorter. In fact, after the first report at ~3.6 Ma (Leporidae indet.), leporids “appear” again in the fossil record at ~2.1/1.9 Ma (*Sardolagus obscurus*). Studied remains of *Sardolagus* cover ~1 Ma. However, it is quite likely that: (1) slightly younger leporid remains recovered in the Monte Tuttavista infillings pertain too to *Sardolagus*, and that (2) Leporidae indet. from Capo Mannu D1 is related to *Sardolagus*. In this case, the persistence of this genus would be noticeably longer (~3.6-0.8 Ma).

Open questions and further investigations

As usual, new data solve some questions but open new problems or new perspectives of study. We envisage a focus of the future studies about Italian fossil lagomorphs in the following topics:

- the lower Messinian *Prolagus* cf. *apricenicus* from Capo di Fiume (Abruzzi-Apulia PB) is one of the very few articulated, almost complete skeletons of *Prolagus* available at present. A morpho-functional study would clarify several questions about the

life-style of *Prolagus*. The analysis of its teeth, now hidden, will provide insights about the taxonomic position of this specimen, inferred on a palaeogeographical basis (Mazza et al. 1995).

- *Trischizolagus* sp. from the evaporitic Messinian of Brisighella needs to be studied in order to understand its phylogenetic affinity with other European species, and to reconstruct the dispersal path followed by the genus to achieve its pan-European distribution.

- Apart from the taxonomic revision, necessary to confirm that *Prolagus* aff. *sorbinii* and *P. savagei* pertain to the same species, it will be necessary to clarify their relationship with *P. depereti* López Martínez in López Martínez & Thaler 1975, distributed in the MN15 of southern France (See Angelone & Rook 2012: 140, 141). The result will have noticeable palaeobiogeographical repercussions (see Angelone et al. 2019).

- The reports of remains attributed to the genus *Lepus* in Italy need a complete revision, necessary to understand the distribution of the genus in the Italian Pleistocene.

These tasks are important not only for the accounting of palaeobiodiversity and the updating of biochronological data, but also to better understand the dispersal events and the palaeobiogeographical framework of western central Europe during the late Neogene-Pleistocene.

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