C. R. Palevol 18 (2019) 1025–1040

Contents lists available at ScienceDirect

Comptes Rendus Palevol

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General Palaeontology, Systematics, and Evolution (Vertebrate Palaeontology)

Contribution of fossil Lagomorpha (Mammalia) to the refinement of the late Miocene–Quaternary palaeobiogeographical setting of Italy

Contribution des lagomorphes fossiles (Mammalia) à la redéfinition des connaissances paléogéographiques relatives au Miocène supérieur–Quaternaire de l'Italie

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ARTICLE INFO

Article history:
Received 17 June 2019
Accepted after revision 7 October 2019
Available online 21 November 2019

Handled by Lars vd Hoek Ostende

Keywords:
Ochotonidae
Leporidae
Stem lagomorphs
Neogene
Pleistocene
Insularity
Continental endemisms

Mots clés :
Ochotonidae
Leporidae
Souche des lagomorphes
Néogène

ABSTRACT

Fossil lagomorphs are very useful palaeogeographical indicators. In the last 15 years, several papers centered on fossil lagomorphs contributed to improve the Italian late Miocene–Quaternary palaeogeographical setting, solving palaeobiogeographical enigmas debated for decades, and providing new, challenging palaeogeographic data. The high number of endemic fossil lagomorphs of Italy is due in part to its complex tectonic history (insular endemisms), and in part to the semi-isolation and the physiography of the Peninsula (continental endemisms). In Italian lagomorphs, a direct causal relationship between dispersal and turnovers is not observed, except for the Toringian. Actually, species replacements are customarily due to archipelago effect (late Miocene), phyletic speciation (Pliocene of Sardinia and Italian mainland) or occur after the extinction of older congeneric species (early Pleistocene).

RÉSUMÉ

Les lagomorphes fossiles sont très utiles comme indicateurs paléogéographiques. Au cours des 15 dernières années, plusieurs études centrées sur les lagomorphes fossiles ont conduit à l'amélioration des connaissances paléogéographiques relatives au Miocène supérieur–Quaternaire italien ainsi qu'à la résolution de problèmes paléobiogéographiques

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https://doi.org/10.1016/j.crpv.2019.10.002
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Pléistocène
Insularité
Endémismes continentaux

de longue date, et ont fourni des nouvelles données qui ouvrent des perspectives très intéressantes. Le nombre élevé de lagomorphes fossiles en Italie résulte en partie de l'histoire tectonique complexe (les endémismes insulaires) de ce pays et en partie de son isolement péninsulaire ainsi que de sa physiographie (endémismes continentaux). Parmi les lagomorphes italiens, il n'a pas été observé de causalité directe « dispersion → turnover », sauf au Toringien. On constate qu'en Italie les remplacements des espèces sont liés à l'effet archipel (pendant le Miocène supérieur) ou à la spéciation phylétique (dans le Pliocène de Sardaigne et de l'Italie continentale), ou bien se vérifient après l'extinction d'espèces congénériques préexistantes (Pléistocène inférieur).

1. Introduction

Lagomorphs are very abundant in European small mammal assemblages, especially from Miocene onwards (López Martínez, 2001) and they are of the highest importance in palaeobiogeographical reconstructions (see Angelone, 2008a for details and examples). In fact, lagomorphs need an emergent land connection to cross sea traits, and they are very sensitive even to minor geographical hindrances (Angelone, 2007, 2008a, 2008b; Angelone and Čermák, 2015; Angelone and Hír, 2012; Angelone and Veitschegger, 2015; Angelone et al., 2015, 2017). Thus, they are very useful (1) to individuate the nature of a dispersal pathway, (2) to identify insular or continental endemisms not recorded by other taxa, and (3) to provide additional details to palaeogeographical reconstructions.

In the last 15 years, there was a renewed interest in European fossil lagomorphs; thus, the taxonomy of Italian taxa underwent important improvements. Angelone et al. (in press) already provided an updated taxonomic overview and the relative biochronological framework, whereas a palaeobiogeographical state of the art is addressed here. The aims of this paper are (1) to sum up palaeogeographical novelties arisen from the study of Italian fossil lagomorphs, and (2) their integration in the Italian palaeobiogeographic framework since the early-middle Turolian (oldest record of Italian lagomorphs) to the Holocene.

2. Material and methods

For the taxonomic assignments and the biochronological distribution of Italian lagomorphs, we refer to Angelone et al. (in press with references).

The palaeobiogeographical framework of Italian late Miocene–early Pleistocene illustrated in Fig. 1

is based on the following papers: Cocozza et al. (1974) and Esu and Kotsakis (1983) for the reconstruction of emerged lands in Sardinia and Corsica during the late Miocene–Pleistocene; Vai (1988) for the reconstruction of the southern Alpine foothill from the Pliocene to the early Pleistocene; Boccaletti et al. (1990) for the main lineaments in the Italian late Miocene, in order to infer the southern limit of the Tusco-Sardinian PB and the main fault systems along which the islands of the palaeobioprovince were periodically disrupted and rebuilt together; Faccenna et al. (1996) for the architecture and position of the extensional system of the Tyrrhenian Sea during the late Miocene; Masini et al. (2002) for the early Messinian of Gargano area; Rook et al. (2006) for the evolution of the northern peri-Tyrrhenian area from the Tortonian to the Messinian; Marra (2013) for the palaeogeographical setting of Sicily during the Pleistocene; Patacca et al. (2013) for the reconstruction of the Apulian Platform during the Tortonian.

Following the recommendations of the International Commission of Stratigraphy, the first letter of informal subepochs is not capitalized.

Abbreviations: FC/FsC: Faunal Complex, Faunal sub-Complex; PB: palaeobioprovince.

3. Lagomorph palaeobiogeography of Italy: late Miocene

The oldest Italian lagomorph record dates back to the late Tortonian, at ~8.3 Ma (Section 3.1), corresponding to the early Turolian. In this time frame (Fig. 1A) (Kotsakis et al., 1997; Rook et al., 2006, 2008 with references), the Italian territory as we know it today was fragmented and partly submerged:

- Sardinia and Maritime Tuscany represented an insular domain called the Tusco-Sardinian PB; the above-mentioned earliest Italian fossil lagomorphs come from there;
- Abruzzi and Apulia formed the homonymous, insular palaeobioprovince (Abruzzi–Apulia PB);
- some sectors of today's Apennine chain were emerged, as attested by stratigraphic evidences, and by a palaeontological evidence: a sole reports of a lower jaw of *Acerorhinus*, a genus of MN9–12 age of Asian and eastern European distribution reworked in early Pleistocene marine deposits (Pandolfi et al., 2013);
- most likely, other sectors were emerged, as parts of Calabria and Sicily, and the southern foothills of Alps (as highlighted in Fig. 1A), but no fossil evidence is available at present.

After ~6.7 Ma (Fig. 1B) (Kotsakis et al., 1997; Marra et al., 2011; Masini et al., 2008; Rook et al., 2006, 2008):

- the Tusco-Sardinian PB was disrupted and Maritime Tuscany connected to Italian and European mainlands, leaving Corsica and Sardinia isolated;

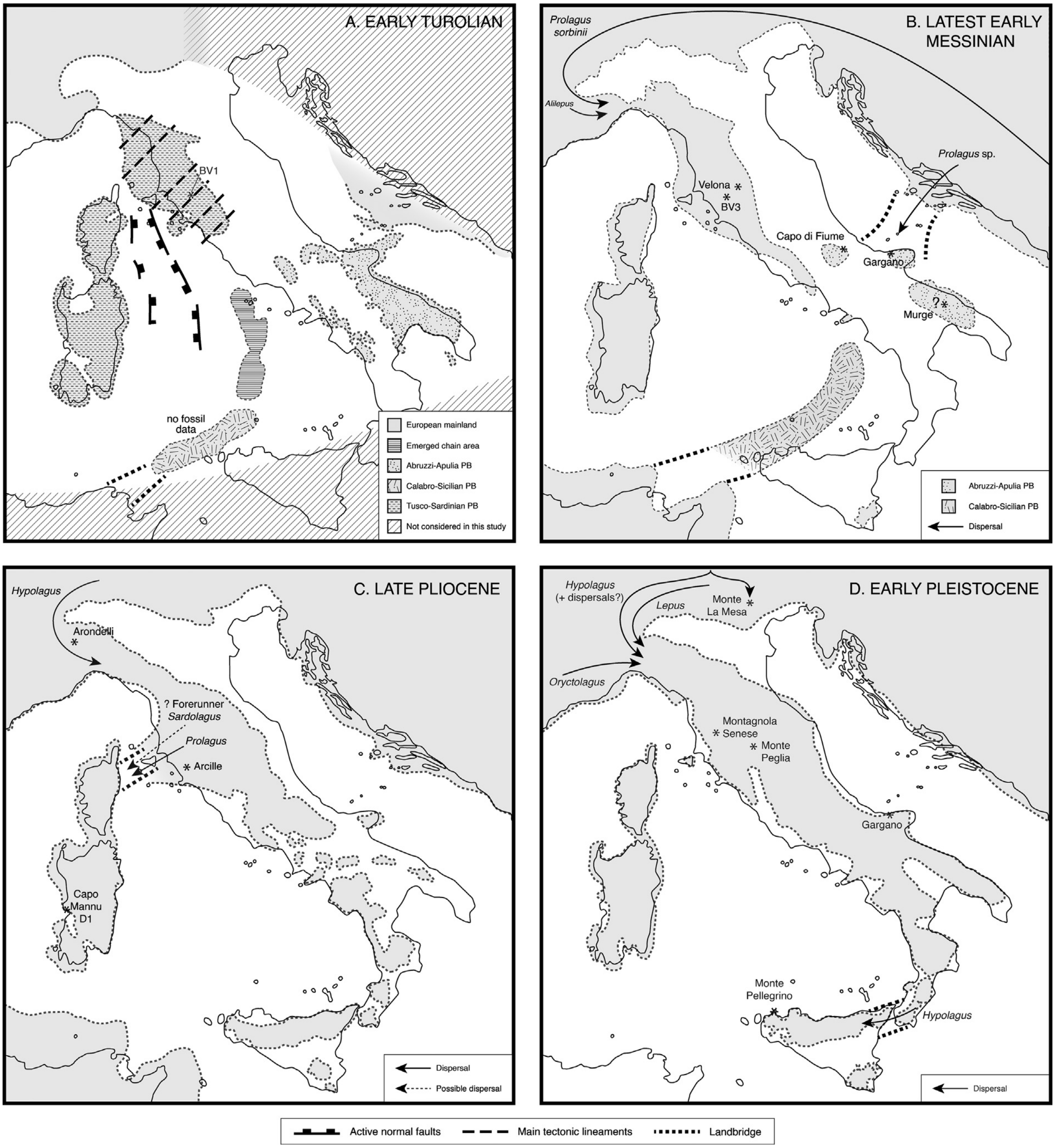

Fig. 1. Tentative reconstruction of the distribution of emerged lands relative to the Italian late Miocene–Pleistocene with emphasis on the contribution of fossil lagomorphs. **A**. The Tusco-Sardinia PB was isolated for almost the entire Miocene. It was fragmented into two main subdomains, of which the eastern one (Tuscanian subdomain) was further fragmented to form an archipelago. The configuration of the archipelago was quite variable, even in relatively short timespans (Section 3.1), thus we preferred to illustrate the area unfragmented and to depict on it the main tectonic lineaments. **B**. The lagomorphs of the Abruzzi–Apulia PB confirm its fragmentation in an archipelago, and highlight the presence of a connection with mainland (represented by the Balkan area) in the early Messinian (~6.5 Ma). Northwestern and central Italy become connected to European mainland, thus allowing the dispersal of lagomorphs of both western and eastern European affinity. **C**. Oldest dispersal into Italy of *Hypolagus* from central Europe through the northwestern passage. Sardinian endemic *Prolagus* pinpoint a dispersal from Italian mainland at the earliest late Pliocene by means of an emergent land connection. We depict here one of the hypotheses for the dispersal of the forerunner of *Sardolagus* to Sardinia. **D**. Several new taxa dispersed into Italy from the European mainland. The oldest dispersal involves *Oryctolagus* from western Europe (~2.5 Ma); follow several early Biharian dispersals of *Hypolagus brachygnathus* from central Europe; *Lepus* appears in Italy at ~1 Ma, dispersing through central Europe from eastern sectors. *Hypolagus* reaches Sicily through an emergent land connection. * Main lagomorph-bearing fossiliferous sites.

- the Abruzzi–Apulia PB persisted;
- there is hard evidence of the existence of the Calabro-Sicilian PB as a peninsula of North Africa available from scattered and scanty fossils consisting of bone fragments of large continental mammals.

3.1. Tusco-Sardinian PB

The age of the fossil mammals of the Tusco-Sardinian PB cover a time span of ~1.6 Ma (~8.3–6.7 Ma; Fig. 2) (Benvenuti et al., 2015; Rook et al., 2011; see also Cirilli et al., 2016). The palaeobioprovince is, however, much older, and late Miocene palaeocommunities were the result of several dispersal events. The last two occurred: (1) at ~8.3–8.1 Ma, age of the V0 assemblage, attested by the presence of a non-endemic European murid (Engesser, 1989), and (2) after ~7.1–6.7 Ma, age of the V2 assemblage, attested by the presence of new taxa of European affinity (Benvenuti et al., 2001, 2015). Older dispersal events from Europe, and probably from Africa, are attested by other endemic taxa (Abbazzi et al., 2008). Nevertheless, until now, it was impossible to date them and, consequently, to understand when the Tusco-Sardinian PB first became isolated.

A revision of the stem lagomorph *Paludotona* provided a minimum age constraint for the onset of insular conditions in the Tusco-Sardinian PB. The continental ancestor of *Paludotona* was individuated in a European species not younger than MN1–2 (Angelone et al., 2017). As lagomorphs seem incapable to actively cross water straits (Angelone, 2007), MN1–2 may represent the upper constraint for the age of the separation of the Tusco-Sardinian PB from continental Europe, or the age of the (?)last landbridge connection to Europe before MN13.

During the Miocene, the Tusco-Sardinian PB received dispersals from mainland, as the composition of the assemblages attests to a polyphasic origin (see Masini et al., 2008 with references). Nevertheless, no other lagomorph apart *Paludotona* is present in its fossil record. Particularly remarkable is the absence of *Prolagus*, a very widespread genus in European Miocene (López Martínez, 2001) and possibly a pioneer taxon, capable to disperse in insular domains immediately after an emergent land connection is available (see Sections 3.3 and 4.2 for examples relative to Italy). If this may indicate that the Tusco-Sardinian PB was not connected to European mainland through a landbridge connection (= corridor dispersal *sensu* Van der Geer et al., 2010) since MN1–2 until MN13 (= at least 13 Ma), is a hypothesis that it will be worth to test. When Tuscany was joined to the Italian mainland (~6.5 Ma), new lagomorphs dispersed in the area (Section 3.3).

The geographical distribution of the *Paludotona*-bearing fossil sites is peculiar, as they are concentrated in modern maritime Tuscany only. No report of *Paludotona* is available from Fiume Santo, a fossil site located in Sardinia, i.e. the western side of the Tusco-Sardinian PB. The fossil content of Fiume Santo stands out also for its rodent composition (Casanovas-Vilar et al., 2011). This pattern can be explained by an ecological difference between the two sides of the palaeobioprovince, but Angelone et al. (2017) argued that a more suitable hypothesis is to imagine the Tusco-Sardinian PB as divided into two subdomains (Fig. 1A): (1) a Sardinian subdomain corresponding to modern Sardinia + Corsica, and (2) a Tuscanian subdomain comprising maritime Tuscany. The geographical hindrance between the two subdomains that prevented the dispersal of lagomorphs and made the interchange of rodents difficult, in spite of the geographical closeness, may have been related to the opening of the Tyrrhenian Sea. According to Mauffret et al. (1999), the opening of the northern Tyrrhenian Sea started in the Oligocene–early Miocene, coeval with the rifting of the Ligurian-Provençal Basin; it stopped almost immediately after, and then restarted again in the late Tortonian (Moeller et al., 2014). This is congruent with the existence of a seaway that encumbered lagomorph dispersal through the entire palaeobioprovince since its establishment as an isolated domain.

Further insights about the palaeogeography of the Tuscanian subdomain emerged after the study of the phylogeny and evolution of *Paludotona*. Actually, the revision of the genus (Angelone et al., 2017) highlighted some apparent inconsistencies: (1) *Paludotona etruria* from local biochron V1 is more advanced and larger than the younger species *Paludotona minor* recovered from local biochron V2; (2) the oldest known specimens of the genus, classified as *P.* aff. *minor*, were more similar to the younger ones (*P. minor*, V2) than to those that should have been the “intermediate” stage (*P. etruria*, V1). In a small insular area as the Tuscanian subdomain, and in a limited time span as the one covered by the available findings (~1.6 Ma), this can be explained only assuming the fragmentation of the domain in an archipelago, in which the different islands

Fig. 1. Vue d’ensemble des nouvelles données paléogéographiques relatives au territoire italien, fournies par l’étude de lagomorphes fossiles. Tentative de reconstitution de la distribution des terres émergées en Italie pour la période Miocène supérieur–Pléistocène, l’accent étant mis sur la contribution des lagomorphes fossiles. **A.** Le bloc Toscane–Sardaigne a été isolé pendant presque tout le Miocène. Il a été fragmenté en deux principaux sous-domaines, dont l’un (le sous-domaine toscan) a été fragmenté pour former un archipel. La configuration de cet archipel était très variable, et même pour des périodes de temps relativement courtes (Section 3.1), nous avons donc préféré illustrer le domaine non fragmenté et en figurer les principaux linéaments tectoniques. **B.** Les lagomorphes du bloc Abruzzes–Apulie confirment la fragmentation de ce dernier en un archipel et mettent en évidence la présence d’une connexion avec le continent (représenté par la zone des Balkans) au Messinien inférieur (~6,5 Ma). L’Italie nord-occidentale et centrale se connecte au continent européen, permettant ainsi la dispersion de lagomorphes présentant des affinités avec l’Europe occidentale et orientale à la fois. **C.** Dispersion la plus ancienne vers l’Italie d’*Hypolagus* à partir de l’Europe centrale au travers du passage nord-occidental. Le *Prolagus* endémique en Sardaigne permet de repérer une dispersion depuis le continent italien au début du Pliocène supérieur grâce à une connexion avec une zone émergée. Nous indiquons ici l’une des hypothèses possibles pour la dispersion du précurseur *Sardolagus* vers la Sardaigne. **D.** Différents taxons se dispersent en Italie à partir du continent européen. La dispersion la plus ancienne est celle d’*Oryctolagus* de puis l’Europe occidentale (~2,5 Ma). D’autres dispersions d’*Hypolagus brachygnathus* depuis l’Europe centrale suivent au Biharien inférieur. *Lepus* apparaît en Italie à ~1 Ma, à partir de zones orientales au travers de l’Europe centrale. *Hypolagus* atteint la Sicile grâce à une connexion avec une terre émergée. * Principaux sites fossilifères de lagomorphes.

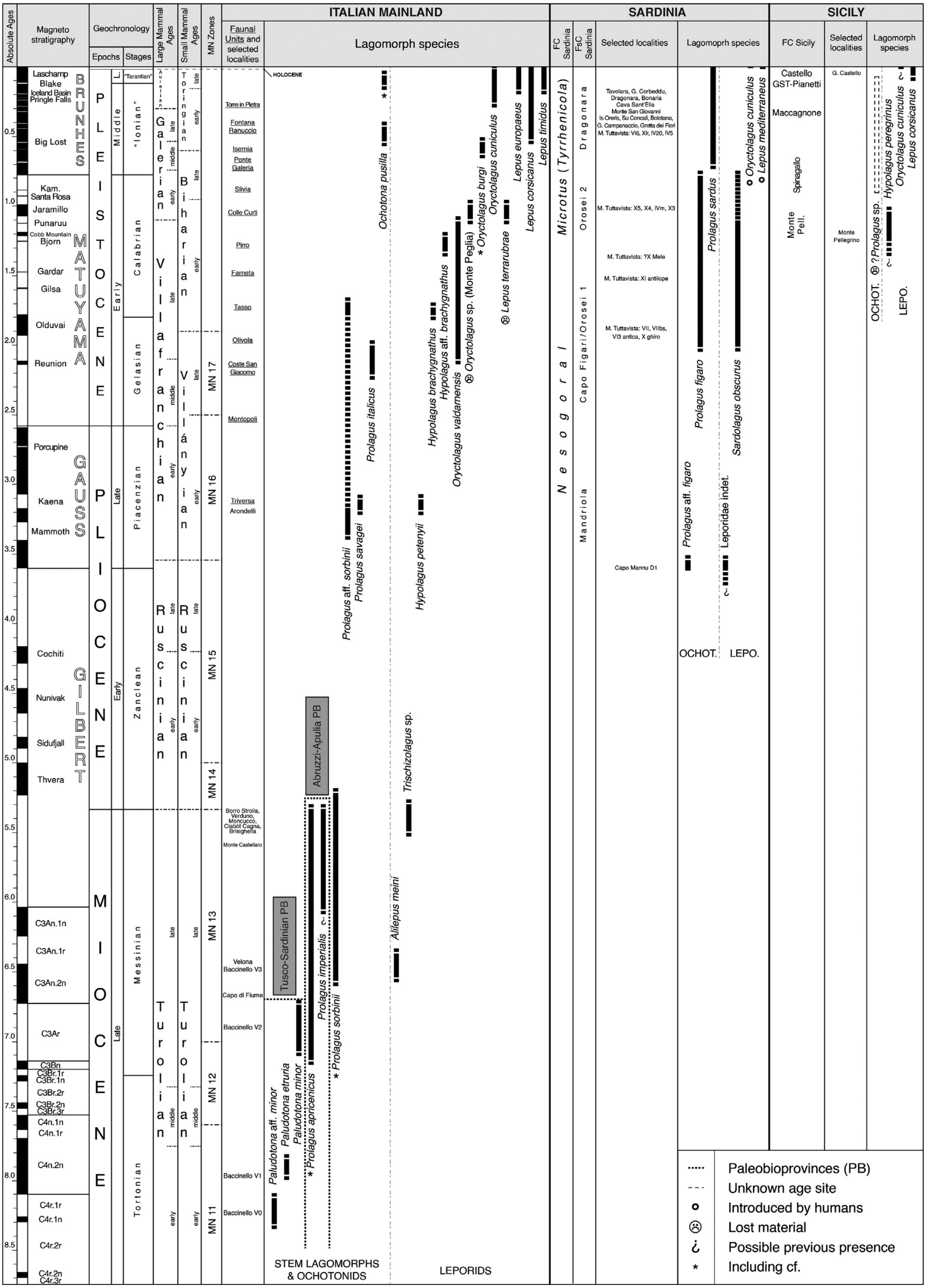
Absolute Ages
Magneto stratigraphy
Geochronology
Epochs
Stages
Large Mammal Ages
Small Mammal Ages
MN Zones
ITALIAN MAINLAND
Faunal Units and selected localities
Lagomorph species
SARDINIA
FC Sardinia
FsC Sardinia
Selected localities
Lagomoprh species
SICILY
FC Sicily
Selected localities
Lagomorph species
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
Laschamp
Blake
Iceland Basin
Pringle Falls
Big Lost
BRUNHES
Kam.
Santa Rosa
Jaramillo
Punaruu
Cobb Mountain
Bjorn
Gardar
Gilsa
Olduvai
Reunion
MATUYAMA
Porcupine
Kaena
Mammoth
GAUSS
Cochiti
Nunivak
Sidufjall
Thvera
GILBERT
C3An.1n
C3An.1r
C3An.2n
C3Ar
C3Bn
C3Br.1r
C3Br.1n
C3Br.2r
C3Br.2n
C3Br.3r
C4n.1n
C4n.1r
C4n.2n
C4r.1r
C4r.1n
C4r.2r
C4r.2n
C4r.3r
PLEISTOCENE
PLIOCENE
MIOCENE
L
Middle
Early
Late
Early
Late
"Tarantian"
"Ionian"
Calabrian
Gelasian
Piacenzian
Zanclean
Messinian
Tortonian
Aurelian
Galerian
Villafranchian
Ruscinian
Turolian
Toringian
Biharian
Villányian
late
middle
early
MN 17
MN 16
MN 15
MN 14
MN 13
MN 12
MN 11
HOLOCENE
Torre in Pietra
Fontana Ranuccio
Isernia
Ponte Galeria
Slivia
Colle Curti
Pirro
Farneta
Tasso
Olivola
Coste San Giacomo
Montopoli
Triversa
Arondelli
Borro Strolla, Verduno, Moncucco, Ciabòt Cagna, Brisighella
Monte Castellaro
Velona
Baccinello V3
Capo di Fiume
Baccinello V2
Baccinello V1
Baccinello V0
Ochotona pusilla *
Prolagus aff. sorbinii
Prolagus savagei
Prolagus italicus
Hypolagus petenyii
Hypolagus brachygnathus
Hypolagus aff. brachygnathus
Oryctolagus valdarnensis
☹ Oryctolagus sp. (Monte Peglia)
* Oryctolagus burgi
Oryctolagus cuniculus
☹ Lepus terrarubrae
Lepus corsicanus
Lepus europaeus
Lepus timidus
Trischizolagus sp.
Alilepus meini
Abruzzi-Apulia PB
Tusco-Sardinian PB
Paludotona aff. minor
Paludotona etruria
Paludotona minor
* Prolagus apricenicus
Prolagus imperialis ¿
* Prolagus sorbinii
STEM LAGOMORPHS & OCHOTONIDS
LEPORIDS
Microtus (Tyrrhenicola)
Nesogoral
Dragonara
Orosei 2
Capo Figari/Orosei 1
Mandriola
Tavolara, G. Corbeddu, Dragonara, Bonaria
Cava Sant'Elia
Monte San Giovanni
Is Oreris, Su Concali, Bolotana, G. Campanaccio, Grotta dei Fiori
M. Tuttavista: VI6, XIr, IV20, IV5
M. Tuttavista: X5, X4, IVm, X3
M. Tuttavista: ?X Mele
M. Tuttavista: XI antilope
M. Tuttavista: VII, VIIbs, VI3 antica, X ghiro
Capo Mannu D1
Prolagus aff. figaro
Prolagus figaro
Prolagus sardus
Leporidae indet. ¿
Sardolagus obscurus
o Oryctolagus cuniculus
o Lepus mediterraneus
OCHOT.
LEPO.
Castello
GST-Pianetti
Maccagnone
Spinagallo
Monte Pell.
G. Castello
Monte Pellegrino
OCHOT. ☹ ?Prolagus sp. ¿
Hypolagus peregrinus ¿
Oryctolagus cuniculus ¿
Lepus corsicanus
LEPO.
····· Paleobioprovinces (PB)
- - - Unknown age site
o Introduced by humans
☹ Lost material
¿ Possible previous presence
* Including cf.

Fig. 2.

experienced episodes of connection and subsequent isolation that led to allopatric speciation. The hypothesis of a Tusco-Sardinian palaeoarchipelago was briefly hinted by Engesser (1989), though never developed or tested.

3.2. *Abruzzi–Apulia PB*

The age(s) of the faunal dispersal(s) into the Abruzzi–Apulia PB still is a matter of discussion (De Giuli et al., 1987; Freudenthal and Martín-Suárez, 2010; Freudenthal et al., 2013; Masini et al., 2002, 2010, 2013; Mazza, 2013; Mazza and Rustioni, 2008; Patacca et al., 2008a, 2008b; Savorelli et al., 2017; van den Hoek Ostende et al., 2009 with references).

As for lagomorphs, the hypothesis of a Balkan origin of the insular endemics from the Terre Rosse of Gargano (*Prolagus apricenicus* and *Prolagus imperialis*; Mazza, 1986) was validated both phylogenetically and palaeogeographically:

- cladistic analyses confirm that *P. apricenicus* and *P. imperialis* pertain to an eastern European clade that dates back at least to the early part of the late Miocene (Angelone and Veitschegger, 2015; Angelone et al., 2015);
- the dispersal of the ancestor of the endemic *Prolagus* of Gargano was pinpointed to the early Messinian regression, when the emersion of structural highs in central-southern Adriatic Sea formed a landbridge (Fig. 1B) (Angelone, 2007).

The inferred age of dispersal is consistent with the lack of lagomorphs in the oldest localities of Gargano (Masini et al., 2013). Thus, among the models proposed for the origin of the Gargano Terre Rosse faunal assemblages, lagomorphs support the ‘polyphasic’ hypothesis, which assumes that the assemblage was built up after several diachronous dispersal events (Masini et al., 2002; Savorelli et al., 2017 with references).

Lagomorphs confirm the fragmentation of the Abruzzi–Apulia PB in an archipelago suggested since the earliest papers on the subject (De Giuli et al., 1987; Freudenthal, 1971, 1976). The existence of a hypothetical transitional form between *P. apricenicus* and *P. imperialis* never found in the fossil record is quite unlikely. In fact, the “sudden” appearance of *P. imperialis* and its “superposition” with *P. apricenicus* in youngest infillings (= no substitution of the older species by the younger one) definitively excludes anagenesis. These evidences fit instead with the dispersal of *P. imperialis* to Gargano from another island of the archipelago. Cladistics analyses indicate *P. apricenicus* and *P. imperialis* as sister species (Angelone et al., 2015), a phylogenetic scenario consistent with an allopatric speciation of populations derived from a common European ancestor, due to the fragmentation of the palaeobioprovince in several islands.

In Fig. 1B, we represented the Abruzzi–Apulia PB during MN13 as divided in three main domains corresponding to Abruzzi, Gargano, and Murge. As indicated above, Gargano yields continental vertebrates of MN13 age, thus there is no doubt it was dry land. Tectonic and sedimentological data attest that the Murge area was an emerged land in MN13 (see De Giuli et al., 1987). No studied record of continental vertebrates is available from the Murge area, but Freudenthal (1971, p. 5) affirms that faunas “comparable if not identical” to those of the Gargano assemblages were found “in a limestone quarry between Barletta and Andria, on the Murge highland”. As for the Abruzzi, the only evidence that there still were land mammals in this sector, at least until the early pre-evaporitic Messinian, is the partial skeleton of *Prolagus* found in shallow marine sediments just above the *Bulimina echinata* FOD ($\sim$6.8 Ma in the Mediterranean; Mazza et al., 1995). The specimen was attributed to *P.* cf. *apricenicus* on a biochronological and palaeogeographical basis, and represents the sole report of *Prolagus* out of Gargano in the Abruzzi–Apulia PB. Further studies of the specimen may provide data to refine the reconstructions of the Abruzzi–Apulia PB, and verify (1) if Abruzzi was separated from Gargano during the whole Messinian, and (2) if this subdomain may be the source of *P. imperialis*.

The leporids of the early Pleistocene of Gargano (Section 5.1) are not related to MN13 assemblages. Actually, the latest Miocene assemblages of Abruzzi–Apulia PB became extinct in the earliest Pliocene due to a marine transgression that submerged the area (De Giuli et al., 1987).

3.3. *Mainland Italy*

The building of the Italian Peninsula dates back to the pre-evaporitic Messinian (MN13). The appearance of eastern and western European taxa in northern and central-western Italy provides indirect evidence of a connection with mainland through a north–west pathway (Fig. 1B). Both leporids and ochotonids were recorded in the oldest post-connection fossil sites of the Italian Peninsula (Angelone, 2007; Angelone and Rook, 2011), as well as several other land mammal dispersed from mainland Europe, attesting that the land connection was “immediately” configurated as a corridor.

MN13 ochotonids of the Italian mainland are represented by *Prolagus sorbinii* and related forms (*P.* cf. *sorbinii*) found in northwestern and central Italy (Angelone et al., in press). A systematic revision of *Prolagus* sp. from the post-evaporitic Messinian of Molise (Cosentino et al., 2018) will clarify if the Messinian distribution of *P. sorbinii* has to be extended also to southeastern Italy. At the

Chronological distribution of lagomorph taxa in mainland Italy, Sicily and Sardinia (mod. from Angelone et al. in press). GST-Pianetti: Grotta San Teodoro–Pianetti FC; Monte Pell.: Monte Pellegrino FC.

Fig. 2. Distribution chronologique des taxons de lagomorphes italiens. Distribution chronologique de taxons de lagomorphes dans les terres émergées d’Italie, de Sicile et de Sardaigne (modifié selon Angelone et al., sous presse). GST-Pianetti : Grotta San Teodoro–Pianetti FC ; Monte Pell. : Monte Pellegrino FC.

present state of the art, the palaeodistribution of *P. sorbinii* appears disjoint: the only reliable record of *P. sorbinii* outside the Italian peninsula is from northern Greece, but the locality is younger than Italian reports (Maramena, Messinian/Pliocene boundary; De Bruijn, 1995). Reports of *P. sorbinii* from the Ruscinian of Moldova and Ukraine (Tesakov and Averianov, 2002) must be reconsidered. The mainstream hypothesis is that *P. sorbinii* arrived from eastern Europe. The alternative is an "out-of-Italy" hypothesis for the dispersal path of *P. sorbinii*, which implies a dispersal towards Italy of a non-identified European species in the earliest Messinian, its immediate speciation into *P. sorbinii*, and its dispersal from Italy to the southern Balkans. It is more parsimonious to hypothesize that *P. sorbinii* originated in eastern Europe not after the earliest Messinian (due to the presence of a mesial hyperloph on P2, a trans-specific feature not acquired before the Messinian; Angelone and Čermák, 2015). The fact that there is no trace of the westward dispersal path of *P. sorbinii* may be explained by the poor knowledge of eastern and central European lagomorphs. We exclude that *P. sorbinii* entered mainland Italy using a "shortcut" through the Abruzzi–Apulia PB. Apart for its connection with the Balkans in the early Messinian (Section 3.2), the Abruzzi–Apulia PB was an isolated domain, and island hopping is not congenial to lagomorphs. Moreover, cladistic analyses evidence that *P. sorbinii* and *Prolagus* spp. from Gargano are phylogenetically distant, being placed in different clades (Angelone et al., 2015).

Alilepus, the first leporid to reach Eurasia in MN11 (Flynn et al., 2014), is also the oldest Italian leporid (Fig. 2): *Alilepus meini* is present in the pre-evaporitic Messinian of southern Tuscany. The erection of this species excluded the presence of *Hypolagus* in Italy in pre-Pliocene times (Angelone and Rook, 2011). *Alilepus meini*, as well as other coeval mammals of southern Tuscany, is a continental endemic not inherited from the insular endemic Tusco-Sardinian PB. The MN13 palaeophysiography of central Apennine, characterized by several intermontane basins, explains the high incidence of continental endemisms. *Alilepus meini* is phylogenetically close to *A. turolensis* (Angelone and Rook, 2011). The geographical distribution of *A. turolensis* was recently reconsidered as limited to the MN12–13 of Spain and MN13 of France, as the recorded occurrences in the MN12–MN13 of northern Greece need to be re-evaluated (Čermák et al., 2015 and references therein). Thus, *A. meini* can be considered a taxon of western European origin.

The oldest Italian report of *Trischizolagus*, an early leporid of Eurasian distribution, occurs in the post-evaporitic Messinian of eastern-central Italy (De Giuli, 1989), i.e. slightly later than that of *Alilepus*. Another report of *Trischizolagus* is recorded at the Mio/Pliocene boundary in Tuscany (Angelone and Rook, 2012). At present, the specific attribution of Italian *Trischizolagus* is not available, thus its phylogenetic affinities remain problematic. Two possible source species are *Trischizolagus crusafonti* and *Trischizolagus maritsae*, from localities coeval or slightly younger than Italian ones (latest MN13 or MN13/MN14; age of La Alberca and Alcoy N: Garcés et al., 1998; Montoya et al., 2006). Nevertheless, the distribution of the European species is scattered from southwestern Spain to Greece (Čermák et al., 2019); thus the dispersal pathway of *Trischizolagus* to Italy is unknown.

Undetermined leporids of post-evaporitic Messinian of northwestern and southeastern Italy (Moncucco, Cava Stingeti; Angelone et al., 2011; Cosentino et al., 2018) may pertain to *Trischizolagus*, as the distribution of Italian *Alilepus* is limited to endemic contexts of the pre-evaporitic Messinian of southern Tuscany. Further taxonomic insights are needed to avoid unsupported palaeobiogeographic statements.

4. Pliocene (Ruscinian–early Villányian)

During the Pliocene, the Italian Peninsula was built up almost to its current appearance (Fig. 1C). Sardinia was isolated from mainland. Indirect evidences (Section 5.3) suggest that Sicily experienced periodical connections.

4.1. Mainland Italy

The last occurrence of *Prolagus sorbinii*/*P.* cf. *sorbinii* is in the earliest MN14 of Tuscany (Borro Strolla upper synthem). The fossil record of *Prolagus* has an apparent gap until the appearance of *P.* aff. *sorbinii* in the early part of MN16 (Fig. 2) of Tuscany (Arcille), due to the extreme scarcity of early Pliocene continental deposits. The close phylogenetic relationship between *P. sorbinii* and *P.* aff. *sorbinii* excludes another dispersal of *Prolagus* in the late Pliocene. If *P.* aff. *sorbinii* is a synonym of the coeval "*P. savagei*", the geographical distribution of the species will encompass northern and central Italy. It is necessary to verify if *P. depereti* (MN15, southern France) is another synonym of *P. savagei* (Angelone and Rook, 2012). At the present state of the art, *P. savagei*/*P.* aff. *sorbinii* seems an Italian endemic taxon.

The leporid *Hypolagus* appears in northwestern Italy in the early Villányian (Arondelli; Berzi, 1967). The sole available tooth was referred to *H. petenyii*, quite widespread in central Europe during the late Ruscinian–early Villányian (Čermák, 2009). Palaeogeographically, this means that the northwestern passage activated in MN13 continued to be active during the Pliocene, though it is impossible to state if early MN16 represents the exact moment of the attempted dispersal of *H. petenyii* from central Europe to the Peninsula. The extreme scarcity of Italian material of *H. petenyii* may suggest that ecological/climatic factors hindered its dispersal.

4.2. Sardinia

The oldest Sardinian lagomorphs date back to the earliest part of the late Pliocene (Capo Mannu D1) (Fig. 2). Very likely, the undetermined leporid from Capo Mannu D1 is phylogenetically related to the early Pleistocene *Sardolagus obscurus*, thus the discussion about the arrival of leporids in Sardinia will be addressed in Section 5.2.

Taxonomic revisions, further validated by cladistic analyses, recognized the other Capo Mannu D1 lagomorph, the ochotonid *Prolagus* aff. *figaro*, as a descendant of *P. sorbinii*. Consequently, its source area should be the Italian peninsula (Angelone et al., 2015). *Prolagus* aff. *figaro* is very peculiar, because its morphology is intermediate between its continental ancestor and its direct descendant, the insular endemic *P. figaro* (Section 5.2). This stage is extremely rare to be recorded, because in an insular environment the characters of the source species are obliterated in a few generations (see Mein's, 1983 biphasic model). Capo Mannu D1 records the "exact" moment of *Prolagus* dispersal from mainland. Angelone et al. (2015) argue that an emergent landbridge was activated during the early/late Pliocene marine regression.

5. Early Pleistocene–early Middle Pleistocene (late Villányian–Biharian)

5.1. Mainland Italy

There is no Pleistocene report of *Prolagus* in northern Italy (Fig. 2), probably a local effect of the southwards contraction of the geographical distribution of *Prolagus*, which began in the Pliocene (López Martínez, 2001). In the early Pleistocene, while *P.* aff. *sorbinii* persists in Tuscany, a continental endemic Italian species, *P. italicus*, is recorded in Umbria and Latium (Angelone, 2008b; Bona et al., 2015). Cladistic analyses suggest that *P. italicus* derived from the basal stock of *P. sorbinii,* which dispersed into the Italian Peninsula at the beginning of the Messinian (Angelone et al., 2015). If *P. sorbinii* and *P. italicus* existed as separate species already since the Messinian, a palaeobiogeographical hypothesis to be tested is that *P. sorbinii* inhabited northwestern and northern central Italy, whereas *P. italicus* occupied central and southern central Italy. Further taxonomic insights of *Prolagus* sp. from the post-evaporitic Messinian of Molise (Cosentino et al., 2018) may shed light on this topic. The reason of such an early divergence among the populations of *P. sorbinii* that dispersed to Italy is unknown, but the complex Messinian physiography of the Apennine may have played a pivotal role. *Prolagus* aff. *sorbinii* occupied part of the distribution area of its ancestor *P. sorbinii* (Tuscany, but not Piedmont and Romagna), probably due to the above-mentioned southward contraction of the geographical range of *Prolagus*. *Prolagus* did not survive after ~1.5 Ma in continental Italy.

In the earliest Biharian, *Hypolagus* appears again in Italy (Marchetti et al., 2000). The findings of *H. brachygnathus* from northeastern Italy (Fig. 1D) fit in with the westward expansion of *Hypolagus brachygnathus*. This species appears in the late Villányian of Hungary and its distribution area widens at the expense of *H. petenyii*, reaching western France (Čermák, 2009). *Hypolagus brachygnathus* is larger and more advanced than *H. petenyii* and has more cursorially-structured limbs, an advantageous character for the survival in an epoch (Biharian) characterized by a marked shift towards open habitats (Fladerer and Reiner, 1996).

The other Biharian report of *Hypolagus* in the Italian Peninsula is from southeastern Italy (*H.* aff. *brachygnathus*, Pirro Nord, late early Biharian). It belongs to a balanced faunal assemblage established after the sinking of the Garganic portion of the Miocene Abruzzi–Apulia PB and its eventual re-emersion and connection to mainland Italy. The tooth morphology of *H. brachygnathus* from northwestern Italy fits in with that of early European populations (Angelone, 2013). The tooth morphology of *H.* aff. *brachygnathus*, instead, is advanced also compared to that of the European *H. brachygnathus*, but its tooth size is smaller (Angelone, 2013) and it has a lesser cursorial adaptation (Fladerer and Fiore, 2003), suggesting an origin from a basal stock of *H. brachygnathus*. The dispersal that led the ancestor of *H.* aff. *brachygnathus* to southeastern Italy is very probably distinct from the dispersal related to the northeastern record of *H. brachygnathus*. In fact, in the early Pleistocene, the Padanian Gulf would have prevented a direct descent of *Hypolagus* from northeastern to southeastern Italy. The obligatory route to the Italian peninsula was the northwestern passage activated in the early Messinian. The timing of the dispersal of *Hypolagus* into the peninsula is difficult to constrain, as in late MN17 *Hypolagus brachygnathus* already reached the eastern side of the Pyrenean chain (Chaline et al., 2000).

Oryctolagus appears in the Italian fossil record in the late Villányian (~2.3–2.1 Ma; Angelone and Rook, 2012). *Oryctolagus valdarnensis*, apparently endemic of the Italian Peninsula, is distributed in the late Villányian–early Biharian in northern-central to southeastern regions. *Oryctolagus valdarnensis* possibly stemmed from *O. lacosti*, a western European species with isolated findings in Hungary and Greece (Angelone and Rook, 2012; López Martínez, 2008). Indeed, the appearance of *O. valdarnensis* occurs slightly later than the first appearance of *O. lacosti* (~2.5 Ma). The first occurrence of the genus *Oryctolagus* in Italy is delayed with respect to Europe. The oldest species of *Oryctolagus* is *O. laynensis* (~3.5–2 Ma), distributed in southwestern Europe plus some reports from the MN15 of Greece (these latter, however, deserve careful revisions) (Koufos, 2006; López Martínez, 2008). As Italy and Europe were connected since the latest Miocene, the ecological requirements of *O. laynensis* did not fit in with the environments of the Italian peninsula, or its dispersal was prevented by a local hindrance in northwestern Italy.

The occurrence of *O. valdarnensis* and *H. brachygnathus* in the Italian Peninsula follows an opposite pattern with respect to their closest European mainland relatives. In Europe, *H. brachygnathus* is quite frequent, whereas the distribution of *O. lacosti* is scattered. By contrast, in Italy, *O. valdarnensis* is quite common compared to *Hypolagus*.

The dispersal of *Lepus* into the Italian peninsula at the end of the early Biharian (*L. terraerubrae*, now *nomen dubium*, pers. comm. S. Čermák, 2019; see Angelone et al., in press; Monte Peglia lower levels, ~1.0 Ma or possibly slightly earlier; Van der Meulen, 1973; see Angelone et al., in press for age reference) is related to the oldest westward migration of *Lepus* into Europe, started at ~2 Ma. This event, which can be followed during the Biharian of eastern and central Europe (Averianov, 2001), is probably related to climatic/environmental events. Monte Peglia lower levels record a warm phase (Van der Meulen, 1973) and the slightly older assemblage of Deutsch-Altenburg 4B, where Fladerer (1987) reports *L. terraerubrae*, is also related to a warm, dry phase (climatic data from Ivanov, 2007).

Several other late Biharian leporids of northeastern Italy plus one in southern Italy (Bon et al., 1991; Masini et al.,

2005) need to be revised to verify their relationship with the oldest Italian *Lepus*.

5.2. Sardinia

The endemic insular *Prolagus figaro* characterizes the?latest Pliocene–late early Pleistocene of Sardinia. No dispersal event is required to justify the "sudden" appearance of *P. figaro* in the fossil record as previously thought (López Martínez and Thaler, 1975). In fact, *P. figaro* is the direct descendant of the earliest late Pliocene *P.* aff. *figaro* (Section 4.2), and its absence in the Sardinian fossil record of *Prolagus* for ~1 Ma is due to the extreme scarcity of fossiliferous sites of late Pliocene age (Angelone et al., in press).

At ~0.8–0.7 Ma, Sardinia records a most remarkable species turnover and the appearance of *Prolagus sardus* (Angelone et al., 2008; age inferred from Palombo, 2009: fig. 2) (Fig. 2). *Prolagus sardus* is another endemic insular ochotonid of Sardinia (recorded also in Corsica), known since the middle part of the early Pleistocene to the Holocene. The evidence of a direct phylogenetic relationship *P. figaro* → *P. sardus* eliminated the long-debated problems of the continental ancestry of *P. sardus*, of the timing of its presumed arrival in Sardinia, and of the purported presence of a suitable land connection with mainland between Middle and Late Pleistocene.

The?latest Pliocene–late early Pleistocene of Sardinia yielded the leporid *Sardolagus obscurus*. A direct phylogenetic relation between this taxon and Leporidae indet. from Capo Mannu D1 is the most parsimonious hypothesis to cover the ~1 Ma gap in the fossil record (Angelone et al., 2018). This means that there are no dispersal events involving leporids between ~3.6 Ma (Capo Mannu D1) and ~2.1/1.9 Ma (the onset of the Capo Figari/Orosei 1 faunal sub-complex, in which *Sardolagus* is first recorded). The ancestor of *Sardolagus obscurus* underwent such deep changes in the insular domain, that it is impossible to link it to any continental leporid genus. Lacking phylogenetic data, the arrival of the ancestor of *Sardolagus* in Sardinia can not be temporally framed. Angelone et al. (2018) examined several possibilities: the most probable palaeobiogeographical scenario is a dispersal of *Hypolagus* from the Italian mainland at ~3.6 Ma through the landbridge that allowed *Prolagus* to disperse to Sardinia (Fig. 1C). Indeed, *Hypolagus*, though extremely rare, was present in Italy in the early part of the late Pliocene (one report, coeval or slightly younger than Capo Mannu D1; Section 6.1).

5.3. Sicily

The sole assemblage referable to the Monte Pellegrino FC (Biharian) is composed by heterogeneous elements, both for their degree of endemism and for their geographical origin (Marra, 2013; Masini et al., 2008). Part of the assemblage, represented by elements of European and African affinity that arrived in Sicily during the late Miocene, underwent very marked morphological and dimensional modifications due to the permanence in an insular environment. The modifications are so pronounced that it is difficult to individuate the continental source species. Another part of the assemblage is of European origin and shows less marked modifications. The endemic Sicilian leporid *Hypolagus peregrinus* pertains to this latter group. According to Fladerer and Fiore (2003), *H. peregrinus* is related to early representatives of the European taxon *H. brachygnathus*, which dispersed through Italy and eventually to Sicily. The peninsular endemic *H.* aff. *brachygnathus* from the late early Biharian of southeastern Italy (Section 6.1) may represent the closest relative of *H. peregrinus*. Very likely, once they entered Italy, the above-mentioned basal forms of *H. brachygnathus* underwent different degrees and patterns of morphological changes in response to the different palaeogeographical settings they settled in. For example, in the Italian peninsula, where the gene flow with the European source species was possible but obviously difficult, *Hypolagus* started to diverge morphologically from European coeval populations, giving rise to a possible new species (*H.* aff. *brachygnathus*). However, *H.* aff. *brachygnathus* did not develop the morphological and dimensional traits typical of insular endemic mammals as did instead *H. peregrinus*, the species that developed in Sicily after its connection with mainland was over. The Italian remains of *Hypolagus* are insufficient to provide a reliable age constraint to the dispersal of *Hypolagus* either into peninsular Italy (Section 6.1) or Sicily. Fladerer and Fiore (2003) argue that *Hypolagus* reached Sicily through a sweepstake route, but in our opinion the dispersal of *Hypolagus* into Sicily is better explained hypothesizing the presence of an emergent land connection between Calabria and Sicily in the latest Villányian–early Biharian (= time-span of the maximum diffusion of *H. brachygnathus* in Europe).

6. Toringian

6.1. Mainland Italy

Ochotona pusilla, an extant Asian taxon typical of cold, dry steppe is recorded in northeastern Italy in the early Toringian and also in the late Toringian (Abbazzi et al., 2000; Bon et al., 1991). Such reports do not attest to a continuous Toringian record, but represent two different moments of the expansion of the distribution area of *O. pusilla* related to two different cold phases (MIS13–12/MIS11–10, and probably MIS4). *Ochotona pusilla* reached the Iberian Peninsula at 63.4 ± 5.5 ky (Laplana et al., 2015), but it has not been recorded in the northwestern part of the Italian Alps. European Alpine mountain ranges could have presented a barrier for the dispersal of the steppe pika. However, during the cold intervals of the Middle–Late Pleistocene, the forest cover was reduced and large areas of the continental shelf were emerged due to the drop of sea level associated with glaciations (Laplana et al., 2015). The northern part of the Adriatic Sea, which emerged during the glacials, represented an easy dispersal path for *Ochotona* from eastern domains to the southern borders of the Alps.

In the earliest Toringian (~0.6 Ma), *Oryctolagus* appears again in the Italian Peninsula after the gap that followed the extinction of *O. valdarnensis*. The new dispersal is related to a modern stock of *Oryctolagus*, also encompassing the extant rabbit (Angelone, 2013), and is characterized by the appearance in the western part of northern and central Italy of *O. burgi* (Nocchi and Sala, 1997). *Oryctolagus burgi* is an Italian endemic form of quite large size not related to the extant *O. cuniculus* but phylogenetically closer to *O. lacosti* (López Martínez, 2008). Its dispersal into the Italian Peninsula occurred from western domains of Europe. *Oryctolagus burgi* eventually disappeared and, in the Italian record, there is another gap of ~150 ky (Angelone et al., in press). The extant rabbit, *O. cuniculus*, appeared in southern Spain at ~0.6 Ma, associated with a relict faunal assemblage of warmth-loving elements (López Martínez, 2008), and from there invaded France. In the late early Toringian, it is recorded in central Italy (Torre in Pietra lower levels; Caloi and Palombo, 1978). Also for this taxon, the northwestern corridor is the obligatory way to enter the Italian Peninsula. *Oryctolagus cuniculus* is recorded in several Italian fossil sites until MIS3 (Angelone et al., in press). In France, it disappeared earlier, and was absent from the Late Pleistocene to the Early Holocene (Callou, 2003). At the end of the Last Glacial Maximum, its distribution area was limited to the Iberian Peninsula, and probably southernmost Italy and Sicily (Sections 6.3 and 6.4).

In the early Toringian, *Lepus corsicanus* is recorded in northeastern Italy (Visogliano A lower levels; Abbazzi et al., 2000). *Lepus corsicanus* is linked to the basal radiation(s) of hares in Europe and its extant distribution is a relict one (Averianov, 2001; Alves et al., 2008). The report of Visogliano is outside the current Italian distribution of the species (central and southern Italy and Sicily), as a consequence of the arrival of *L. europaeus*, which restricted the area of *L. corsicanus* (Vismara et al., 2014). A reliable palaeodistribution of early *L. corsicanus* in Italy would require a revision of early Toringian specifically undetermined remains of *Lepus*, in order to understand if they are related to *L. corsicanus* or to *L. europaeus*.

The oldest reports of *Lepus europaeus* are difficult to frame: the taxonomic assignment of possible early forms is controversial and the age and correlations with the fossil localities from which they are reported are dubious. The Caucasus seems to be the area from which the species radiated to western Europe. Oldest reports may be of MIS 22–21 (~800 ky, Akhalkalaki; Tappen et al., 2002; age in Baryshnikov, 2002). During the Last Glacial Maximum, the distribution of *L. europaeus* shrunk to southern Europe and was fragmented in at least three *refugia*: the Italian Peninsula, the Balkans, and Anatolia (Fickel et al., 2008). The oldest confirmed reports of *L. europaeus* in the Italian mainland date back to the earliest late Toringian (the several latest early Toringian remains from Veneto need a systematic revision; Angelone et al., in press). The Italian distribution of *L. europaeus* in the late Toringian covers the northern and northern-central sectors, whereas its presence in southern-central and southern Italy needs to be confirmed by a revision.

In the late Toringian, *Lepus timidus* is recorded in northern and central Italy plus one report from southeastern Italy (Angelone et al., in press with references), but, at present, we can not determine if this record represents a continuum or if we are observing different cold pulses. In fact, *L. imidus* is related to cold climates (tundra and taiga environments; Angerbjörn and Flux, 1995), quite different climatic/environmental requirements than *L. europaeus*. Angelone et al. (in press) considered dubious Italian reports of *L. timidus* together with *L. europaeus*. The oldest European record of the species goes back to the Middle Pleistocene (Sudmer-Berg 2; Koenigswald, 1972). During the Late Pleistocene, *L. timidus* was widespread from Portugal to western Ukraine (Averianov, 2001). Its dispersal into Italy may have occurred from both northwestern and northeastern passages, but the northeastern passage was possibly preferential, as, in the cold stages of the Late Pleistocene, ample portions of northern Adriatic Sea were emerged land.

6.2. *Sardinia*

During the Toringian, the endemic *Prolagus sardus* continued to thrive in Corsica and Sardinia, which represent the last *refugia* of the genus (Angelone et al., 2008).

6.3. *Sicily*

The connection of Sicily to mainland Italy, occurred during the Last Glacial Maximum (Marra, 2013), allowed the dispersal of several taxa, and of *Lepus* among them. Those findings are known in the literature as *L. europaeus*, but they very probably pertain to *L. corsicanus* (Angelone et al., in press).

Probably, Sicily represented a *refugium* for *Oryctolagus* during the Last Glacial Maximum: the presence of *O. cuniculus* is reported during the transition Castello FC/Holocene (Masini et al., 2008), in levels of supposed tardiglacial age (the layers may be reworked, though; Mangano and Bonfiglio, 1998), and from levels of early post-glacial age (Villari, 1986).

6.4. *Minor islands*

A combination of eustasy and tectonics caused the connection of Capri with mainland, as attested by an early late Toringian (~250–150 ky) non-endemic, balanced assemblage yielding *Oryctolagus cuniculus*. Between ~150–60 ky, the balanced assemblage was replaced by an insular endemic fauna (Capasso Barbato and Gliozzi, 1995).

In other cases, the connections are mostly driven by eustatic factors (Angelone et al., in press with references):

- Palmaria (La Spezia Archipelago): balanced fauna with two/three leporids (possibly *Oryctolagus* and one/two species of *Lepus*), attesting to a connection with mainland during a non-identified cold interval of the Late Pleistocene;
- Pianosa (Tuscan Archipelago): two Late Pleistocene faunal assemblages. The youngest is a balanced fauna and yielded remains of *Lepus* that arrived during a lowstand of the sea level during a cold stage;
- Elba (Tuscan Archipelago): balanced fossil assemblage with leporids whose age is inferred to late Middle Pleistocene or Late Pleistocene;
- Levanzo: (Aegadian Island) Mesolithic strata record *Oryctolagus*, which probably arrived during the Last Glacial

Maximum marine lowstand, during which it dispersed also in Sicily (Section 6.3);
- San Domino (Tremiti Islands): *O. cuniculus*, present in Late Pleistocene deposits, probably arrived during the Last Glacial Maximum, indirect evidence of the survival of the species after MIS3 in southeastern Italy.

7. Holocene

The Holocene palaeobiogeographic history of Italian lagomorphs has to take into account introductions by humans as game species or as livestock (Angelici et al., 2008; Masseti, 2008; see Angelone et al., in press with references).

As highlighted in Sections 6.1 and 6.4, *Oryctolagus cuniculus* survived the Last Glacial Maximum in the southernmost regions of the Italian Peninsula. Possibly, the rabbit reported at ~8–7 ky in southern Italy (Dini et al., 2008) is not a human introduction, but a relict. This is a novelty for the palaeobiogeographical history of this species, which was thought to survive the Last Glacial Maximum only in the Iberian Peninsula (Angelone et al., in press).

The earliest known Holocene introduction is in the late Neolithic (VI century BP) of Offida (eastern-central Italy; Rustioni et al., 2007). In Sicily, the introduction of rabbits by humans in the Holocene could have interfered with relict populations of wild rabbits (Section 6.3), unless wild rabbit became extinct at the beginning of the Holocene. There is no accordance about the oldest report of the introduction of *Orytolagus* in Sicily: the early or middle Bronze age, Roman times, or the Middle Ages (see Angelone et al., in press with references). In Sardinia, *O. cuniculus* was probably introduced in Roman times (Vigne, 1992), but its presence is attested with certainty since the Middle Ages (Delussu, 1996; Vigne, 1999). An example of human introduction of lagomorphs in minor islands is Nisida (Campania), during the Roman Imperial Age (Barrett-Hamilton, 1912).

The genus *Lepus* in Italy needs a complete revision. However, it can be stated with a fair degree of certainty that, at the beginning of the Holocene, *Lepus europaeus* was the predominant species in northern and central Italy, *L. corsicanus* occupied southern-central and southern Italy (Angelici et al., 2008) and Sicily (Lo Valvo, 2007), and *L. timidus* was distributed in the Alpine region and adjacent areas. In Sardinia, the introduction of *Lepus* by humans dates back to the Bronze Age (~4000–3000 years BP; Masala, 2015), or to the Bronze/Iron Age (~3000 years BP; Wilkens, 2003). Though introduced by humans, the Sardinian hare developed endemic traits, as proven by the results of morphological and molecular studies (Palacios, 1998, Pierpaoli et al., 1999). Nevertheless, it continues to be addressed as a subspecies of *L. capensis* (*L. capensis mediterraneus*; Angelici and Spagnesi, 2008).

8. Discussion and conclusions

8.1. Endemism rate in the Italian territory

In Italy, the number of endemic lagomorphs is particularly high. Among the lagomorphs taxa recorded since the early–middle Turolian to the Toringian, ~65–70% are endemics (Table 1). In pre-Pliocene times, the majority of the endemic taxa were insular endemics (the early–middle Turolian stem lagomorphs of the Tuscanian subdomain of the Tusco-Sardinian PB: *Paludotona etruria*, *P. minor*, *P.* aff. *minor*; the Messinian ochotonids of the Abruzzi-Apulia PB: *Prolagus apricenicus* and *P. imperialis*), whereas one or two were continental endemics (the leporid *Alilepus meini*, developed in the early Messinian intermontane basins of southern Tuscany due to the peculiar local physiographic factors, and possibly the late Messinian leporid *Trischizolagus* sp.). Apparently, *Prolagus sorbinii*, known in the Italian territory since the earliest phases of its continentalization process, was in pre-Pliocene times the only Italian non-endemic lagomorph, as its geographic distribution encompassed also southern Balkans (see Angelone, 2007; Angelone et al., in press with references). Thus, at the end of the Miocene, endemic lagomorphs were almost 90% (more than 60% insular endemics and about 30% continental endemics) of the total number of species.

After the Mio-Pliocene boundary, insular endemic lagomorphs can be found only in the current Italian main islands (*P.* aff. *figaro*, *P. figaro*, *P. sardus*, *Sardolagus obscurus* in Sardinia, *Hypolagus peregrinus* in Sicily). However, the Italian Peninsula continued to host endemic taxa. In fact, during the Villafranchian (= Villányian and most part of the early Biharian), continental endemic lagomorph species still outnumbered those with a wider geographical distribution. Continental endemics represented 40% of the total number of Villafranchian Italian lagomorph species vs. the 20% represented by non-endemics. This means that continental endemics represented almost the 70% of the species that inhabited the Italian Peninsula during the Villafranchian. Interestingly, non-endemic species (*Hypolagus petenyii*, *H. brachygnathus*) occupied the northernmost sectors of Italy, whereas continental endemic taxa were recorded in central and southern Italy (*Prolagus italicus*, *Hypolagus* aff. *brachygnathus*, *Oryctolagus valdarnensis*; *Prolagus savagei*/*P.* aff. *sorbinii* is considered here as an endemic peninsular Italian species, and possibly a vicariant of *P. savagei*/*P.* aff. *sorbinii*, pending a revision of MN14-MN16 *Prolagus* of western Europe).

Since the Galerian (late early Biharian + late Biharian + first part of the early Toringian), the lagomorphs of the Italian Peninsula have lost their endemic fingerprint. In fact, the recorded species have a European distribution (*Lepus* spp., *Oryctolagus cuniculus*) or even Eurasian ranges (*Ochotona pusilla*), except for the continental endemic *Oryctolagus burgi* and *Lepus corsicanus*, and the endemic insular *Prolagus sardus*. Endemics at this point represent about 37% of the total number of species (12% insular endemics and 25% continental endemics).

Thus, it is evident that in Italy endemic lagomorph taxa underwent a reduction since the late Miocene. Insular endemic taxa were affected more significantly than continental endemics. The reduction was progressive, but a couple of main watersheds can be individuated at the Mio-Pliocene boundary and at the beginning of the Galerian. In the first case, the profound palaeobiogeographical changes occurred in the Italian territory during the latest

Table 1
List of the fossil lagomorphs of the Italian Peninsula. *Lepus mediterraneus*, though having acquired insular endemic traits, was not included in the list, as it stemmed from a species artificially introduced by humans in Sardinia. ***Italics and boldface***: late Miocene taxa. *Italics and underlined*: Villafranchian taxa. *Italics*: post-Villafranchian taxa.

Tableau 1
Liste de lagomorphes fossiles de la péninsule Italienne. *Lepus mediterraneus*, bien qu'ayant acquis des caractéristiques insulaires endémiques, n'a pas été inclus dans la liste, comme il est issu d'une espèce artificiellement introduite par l'Homme en Sardaigne. ***Gras et italique*** : taxons du Miocène supérieur. *Italique et souligné* : taxons du Villafranchien. *Italique* : taxons post-villafranchiens.

Italian lagomorph species	Non-endemic	Continental endemic	Insular endemic
Paludotona aff. minor			x
Paludotona etruria			x
Paludotona minor			x
Prolagus apricenicus			x
Prolagus imperialis			x
Prolagus sorbinii	x		
Alilepus meini		x	
Trischizolagus sp.[a]		?x	
Prolagus savagei/*P. aff. sorbinii*		x	
Prolagus italicus		x	
Prolagus aff. figaro			x
Prolagus figaro			x
Hypolagus petenyi	x		
Hypolagus brachyghathus	x		
Hypolagus aff. brachygnathus		x	
Hypolagus peregrinus			x
Oryctolagus valdarnensis		x	
Sardolagus obscurus[b]			x
Prolagus sardus			x
Ochotona pusilla	x		
Lepus terraerubrae	x		
Lepus corsicanus		x	
Lepus europaeus	x		
Lepus timidus	x		
Oryctolagus burgi		x	
Oryctolagus cuniculus	x		
TOTAL	8	7 or 8	10

[a] Considered as an endemic species, pending a systematic revision. *Considéré comme une espèce endémique, en attente d'une révision systématique.*

[b] Including Leporidae indet. from Capo Mannu D1. *Incluant* Leporidae indet., *selon Capo Mannu D1.*

Miocene (i.e. the merging of late Miocene isolated domains into a peninsula connected to European mainland) drastically affected the number of endemic taxa, especially insular endemic ones, and explain the drop in the number of endemisms. In the second case, the framework is more complex. The beginning of the Galerian marked the transition to cooler and more arid climates. This led to major changes in vegetation composition and, consequently, to significant faunal turnovers (Masseti and Sala, 2007, 2011 with references). Thus, indeed the turnover highlighted among lagomorph taxa at the beginning of the Galerian is in line with the well-known Galerian turnover of Italian and European faunas. However, this does not explain satisfactorily the decrease of endemic taxa in the Italian Peninsula. Climate changes affected not only the environment, but also the distribution of emerged lands. In particular, the northeastern passage to Italy became more and more accessible for trans-alpine vertebrates through the Middle and Late Pleistocene (the first steps of the building up of the Po alluvial plain are recorded at the beginning of the Galerian, at ~1 Ma; Bona and Sala, 2016). This is attested by the noticeable increase of the dispersals into Italy recorded during the Middle and Late Pleistocene (Bona and Sala, 2016 with references), as well as by the homogenization of Italian mammal faunas with those of the European mainland.

8.2. *Dispersal pathways*

Prior to the Pliocene, tectonics was the main factor that controlled lagomorph dispersals into the Italian territory, fragmented in several isolated palaeobioprovinces. Italy started its continentalization process connecting to Europe during MN13. However, since the Messinian and until the early Pleistocene, the only dispersal pathway to Italy was the northwestern passage. For *Prolagus*, though arriving from southeastern Europe, it was an obligatory passage. For *Alilepus* and *Oryctolagus*, which came from western European sectors, the northwestern passage was the "natural" dispersal pathway. It is worth to notice that, in spite of the fact that the pathway was activated during the Messinian, some taxa have been having difficulties to reach the Italian peninsula for several hundreds of thousands years. For example, *Oryctolagus* appeared for the first time in the Italian Peninsula with a noticeable delay (more than 1 Ma) with respect to Europe. The same occurred with *Lepus terraerubrae* and, possibly, this was also the case of *Hypolagus petenyii*. Very possibly, the northwestern passage acted as a physiographic and environmental filter due to its position at the piedmont of the Alpine chain.

The northeastern passage was activated relatively recently, thanks to the accumulation of sediments in the Po plain and to the eustatic variations triggered by climate changes. The northeastern passage was very extended during the coldest phases of the Late Pleistocene and especially during the Last Glacial Maximum, when the northern portion of the Adriatic Sea became dry land. This dispersal pathway progressively gained importance and possibly had a major role for the dispersals, during the Toringian, of *Ochotona* and *Lepus*.

Since the Pliocene, Sardinia and Sicily could be reached by lagomorphs only in correspondence of marine regressions. This is also the case of minor Italian islands: the appearance of lagomorphs in their Middle and Late Pleistocene fossil record has to be linked to eustatic variations, with the exception of Capri, where tectonics played a significant complementary role.

8.3. Turnovers

As far as lagomorphs are concerned, the Tusco-Sardinian PB and the Abruzzi–Apulia PB were “closed systems”: they received a dispersal from mainland and, after that, speciations and dispersals were restricted within the archipelago. In the Abruzzi–Apulia PB, there was no actual lagomorph turnover, as the younger species, *Prolagus imperialis*, coexisted with the older one, *P. apricenicus*. In the Tusco-Sardinian PB, each local biochron is characterized by a different species of *Paludotona*; however, the temporal successions of the species can not be interpreted as a series of turnovers, as it represents a series of “snapshots” taken at different times and in different parts (= islands, probably) of the Tuscanian subdomain palaeoarchipelago.

During the early Messinian, when the Tusco–Sardinian PB was disrupted, the territories of the Tuscanian subdomain connected to mainland and recorded a turnover related to the arrival of European lagomorphs, whereas Sardinia continued to experience the “closed system” pattern, except for one episode at the early/late Pliocene boundary (arrival of the forerunner of *P. figaro* and *P. sardus*). Nevertheless, not being an archipelago, the speciation pattern which characterizes Sardinia since the late Pliocene to the Holocene is different than the one observed in the Tusco-Sardinian PB and the Abruzzi–Apulia PB. Actually, in Sardinia, after the earliest late Pliocene dispersal from mainland, the species replacements in leporids and ochotonids were anagenetic. Climatic/environmental changes could have been the trigger of the replacements, but this causal relationship was tested only in the case of *P. figaro* → *P. sardus*.

In the Italian Peninsula, *Alilepus*, *Trischizolagus*, and *Prolagus* did not experience turnovers with European congeneric species, nor with other lagomorphs. Within the genus *Prolagus*, after the early specific divergence (already in the Messinian?) of *P. italicus*, an anagenetic substitution occurred during the early Pliocene within the other lineage (*P. sorbinii* → *P.* aff. *sorbinii*).

The turnovers observed among Italian Plio-Pleistocene leporids (*Hypolagus*, *Oryctolagus*, *Lepus*) seem not to be a consequence of the dispersal of congeneric species from Europe. In the case of *Oryctolagus* and *Lepus*, the turnovers occurred at the beginning of the Toringian, but the early Pleistocene species (*O. valdarnensis*, *L. terraerubrae*) had already became extinct in the late Biharian. In the case of *H. petenyii*/*H. brachygnathus*, due to the poor fossil record, it cannot be stated with certainty if the older species was already extinct when the new dispersal into Italy occurred. The Plio-Pleistocene lagomorph turnover also involved the arrival of *Ochotona* and was very likely related to climatic and environmental changes.

Within the extant species of *Lepus*, appeared in Italy during the Toringian, it is not possible to individuate actual turnovers, but fluctuations of their palaeodistribution related to climate shifts: *L. europaeus* replacing *L. corsicanus* in northern Italy during the late Toringian, and the expansion (probably at the expense of other congeneric species) and the subsequent reduction of the distribution area of *Lepus timidus* in the late Toringian–Holocene.

Acknowledgements

We appreciated the comments of the reviewers (T. Alcover and K. Hordijk) and of the Editor (L. van den Hoek Ostende), and the tactful and encouraging way in which those comments were expressed. We are thankful to S. Čermák for sharing helpful personal knowledge and data.

C.A. was supported by: Visiting Professor grant of the President’s International Fellowship Initiative of the Chinese Academy of Science; Spanish Agencia Estatal de Investigación and the European Regional Development Fund of the European Union (CGL2016-76431-P); CERCA Program, Generalitat de Catalunya; Grant to Department of Science, Roma Tre University (MIUR-Italy Dipartimenti di Eccellenza, ART. 1, C. 314-337 L. 232/2016).

BMS was supported by Xunta de Galicia (ED481B 2018/046, Axudas á etapa postdoutoral da Xunta de Galicia 2018-Modalidade A).

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