

The body mass of *Paludotona* (Lagomorpha, Mammalia): first approach to the ecology of the last stem lagomorph (Tusco-Sardinia palaeobioprovince, Late Miocene)

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ABSTRACT - *Paludotona*, an insular lagomorph genus endemic of the Tusco-Sardinia palaeobioprovince (~8.3-6.7 Ma), is the last representative of the heterogeneous basal group of early lagomorphs. It post-dates the last appearance datum of stem lagomorphs to 6.7 Ma, i.e., by 2.5 my with respect to the previous datum. This makes *Paludotona*, during the Late Miocene, a living fossil thriving in an insular refugium. We have a record of only the last 15% or less of the temporal distribution range of *Paludotona*: in fact *Paludotona* developed in isolation *sensu lato* as a ghost lineage for at least 14 my. *Paludotona* matched the pattern followed by small mammals in insular environments, acquiring a gigantic size with respect to continental ancestors. Its body mass (BM) is here estimated in ~1100 g, i.e., three to five times the BM of the taxa here taken as reference for European MP28-MN1 stem lagomorphs, the group from which *Paludotona* likely stemmed. The reasons for such an enormous BM increase are multiple and interconnected: synecological factors s.l., lower extrinsic mortality, changes in size and degree/pattern of fragmentation of the area of the insular palaeobioprovince, and successive climate changes (which caused a rapid evolutionary pulse followed by a relative stasis following the pattern of Mein's biphasic model). At any rate, through BM estimation and morphological observation we discuss some biological traits of *Paludotona*: there is evidence of increased lifespan (though, at present, not quantitatively determined), and we suspect a change in posture and locomotion caused by the noticeable BM increase.

INTRODUCTION

Inferring biological and ecological traits of fossil species presents several obvious difficulties. Body mass is an indirect key for the assessment of physiological, behavioural, morphological, ecological and life history traits. In fact, body mass is closely correlated with several biological characters (Peters, 1983; Calder, 1984). The study of the body mass of insular endemic lagomorphs of the Neogene of the Western Mediterranean is currently under focus: several recent papers deal with the estimation and variation over time of this proxy (Quintana et al., 2011; Moncunill-Solé et al., 2015, 2016a, b; Moncunill-Solé, 2021), and with the scaling relationships between postcranial bones and teeth (Moncunill-Solé et al., 2021). These studies aim to obtain a general evolutionary framework of the pattern of body size variability in insular endemic lagomorphs, and to detect the influence of parameters other than insularity in body mass variation (climate/ecology - as highlighted in Moncunill-Solé et al., 2016a - or possibly other synecological factors). The Western Mediterranean fossil record includes two insular endemic stem lagomorphs: the genera *Gymnesicolagus* Mein & Adrover, 1982 (originally retrieved in the MN5 of Mallorca and later in sediments dated to the early Tortonian of Menorca; Quintana & Agustí, 2007 and references therein), and *Paludotona* Dawson, 1959

(reported from the latest Miocene of the Tusco-Sardinia palaeobioprovince).

Paludotona has been the subject of a recent revision which highlighted previously unreported details (Angelone et al., 2017): this genus is related to a very primitive stock of European lagomorphs, thrived in an isolated environment diversifying into at least three species, and provided evidence that the Tusco-Sardinia palaeobioprovince actually was an archipelago. Contrary to *Gymnesicolagus*, *Paludotona* is represented also by postcranial remains, which are the most reliable proxies for body mass estimations in Lagomorpha (Moncunill-Solé et al., 2015, 2016b, 2021).

This paper aims to provide for the first time, through the estimation of body mass, palaeobiological and ecological details about a stem lagomorph.

MATERIALS AND METHODS

Abbreviations

GENERAL - BM: body mass; BV0-1-2: local biochrons V0-V1-V2 of the Baccinello-Cinigiano Basin; FAD: first appearance datum; FO: first occurrence datum; LAD: last appearance datum; LO: last occurrence datum.

ANATOMICAL - HL: humerus length; TTDD: distal tibial transversal diameter.

STATISTICAL - N: sample size; %PE: average absolute percent prediction error; r^2 : coefficient of determination; SEE: standard error of the estimate.

INSTITUTIONAL - ICP: Institut Català de Paleontologia “Miquel Crusafont”, Universitat Autònoma de Barcelona; NHM: Natural History Museum London; NHMB: Naturhistorisches Museum Basel; NHMM: Naturhistorisches Museum Mainz.

Materials

The analyzed materials (Fig. 1) consist of a distal fragment of a left tibia (Bac. 793) curated at the Naturhistorisches Museum, Basel (NHMB). The specimen was retrieved in the Trasubbie Valley (Tuscany, Italy) from a site indicated in the NHMB archives as “Über *Cardium* horizon” (Angelone et al., 2017), and dated to the transition between BV1/BV2 Faunal Zones in the Baccinello basin (MN11, early Turolian). The outcrop has

been magnetostratigraphically correlated to the C4n.2n magnetozone (8.108-7.695 Ma; Rook et al., 2011). Bac. 793 is the sole postcranial bone available for the genus, and is referred to *Paludotona* cf. *minor* Angelone, Čermák & Rook, 2017. The fossil fulfils the necessary requirements for carrying out precise body mass (BM) estimations, as it belongs to an adult individual and bears no evidence of pathologies. The skeletal maturity of the tibia is indicated by the complete fusion (lack of suture line) of its distal end.

Comparative materials

Postcranial bones of stem lagomorphs are rare, and their taxonomic attribution in museum collections is often not reliable. Lacking a detailed relevant study, we chose for comparison the only available postcranial remain that can be undoubtedly attributed to a European stem lagomorph: “*Amphilagus*” *wuttkei* Mörs & Kalthoff, 2010

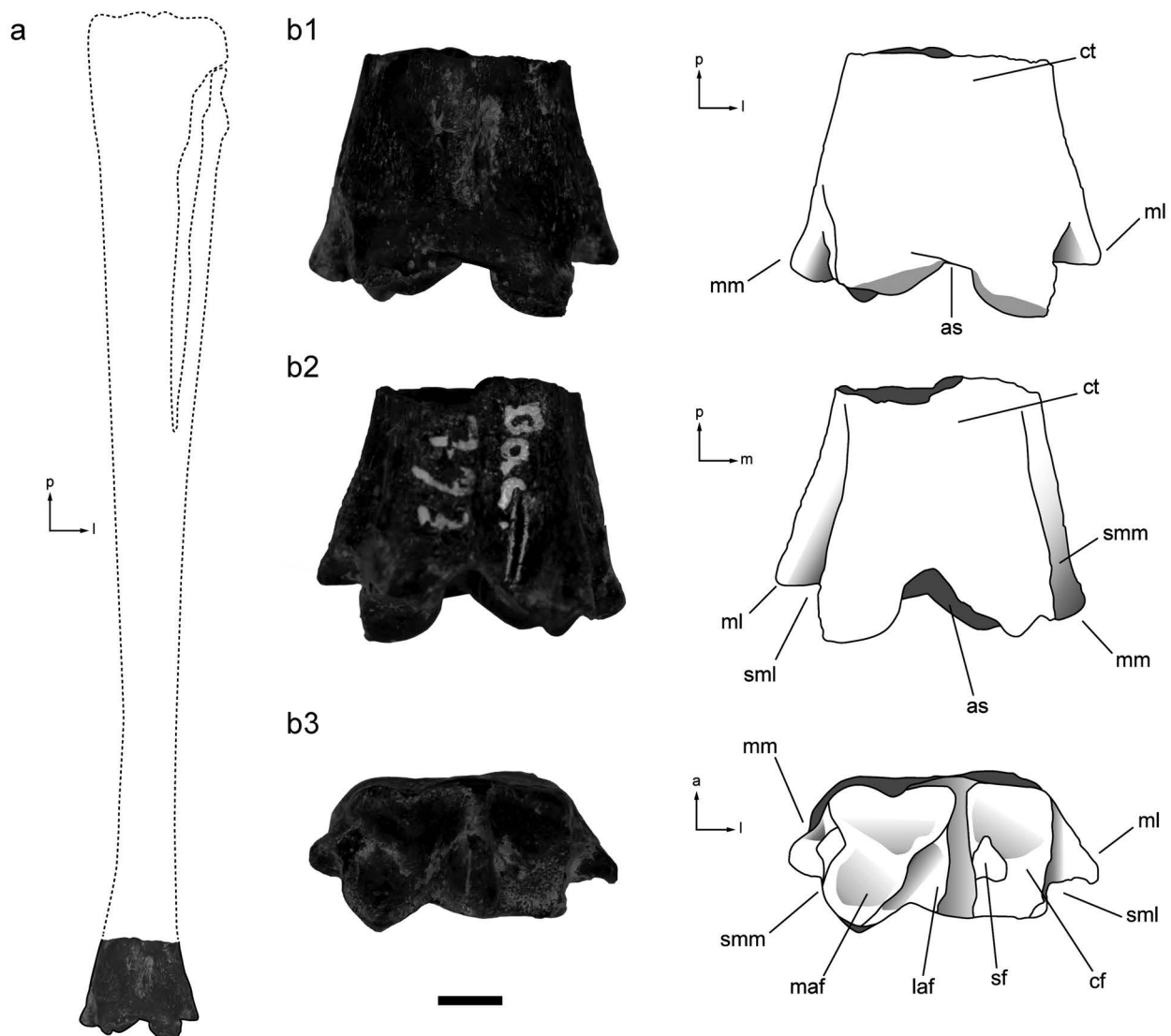


Fig. 1 - Photos and corresponding drawings of distal epiphysis of left tibia NHMB Bac. 793 referred to *Paludotona* cf. *minor*. a) General view (with tibiofibular construction). b1) Anterior view; b2) posterior view; b3) distal view. Scale bar equals 2 mm. a, anterior; as, articular surface; cf, calcaneus facet; ct, corpus tibiofibulae; l, lateral; laf, lateral astragalus facet; maf, medial astragalus facet; ml, malleolus lateralis; mm, malleolus medialis; p, proximal; sf, separation zone between the facets of calcaneum and astragalus; sml, sulcus malleolaris lateralis; smm, sulcus malleolaris medialis.

from Enspel (Germany), Late Oligocene, MP28, encasing sediments dated at ~24.79-24.56 Ma (Mertz et al., 2007). The holotype of this species (NHMM/LS PW2000/5021a) consists of a partial, articulated skeleton preserved in a slab. We used here the HL measurements taken from Mörs & Kalthoff (2010: tabs 1-2, p. 86).

Another HL datum available in literature is a specimen classified as *Amphilagus* Pomel, 1853 vel *Piezodus* Viret, 1925 (NHM 41089; von Meyer, 1870: p. 229) retrieved from Rott (Germany), latest Oligocene, MP30, dated to ~24.2-23.8 my (Kemp et al., 1997).

Neither of the two fossils selected for comparisons pertains to fully adult specimens as theoretically desired, thus they are not perfectly comparable with other data. However, faute de mieux, we consider them the best available materials for comparison with *Paludotona*, though with the due cautions.

Both the selected comparative specimens are dated between MP28-MN1, i.e., the age range in which the ancestor of *Paludotona* should be sought, thus making them good samples to estimate the BM increase of *Paludotona* with respect to related continental forms.

Methodology

Following standardized procedures, measurements of NHMB Bac. 793 were taken from images acquired with a digital camera. Measurements are reported in Tab. 1. The TTDd is considered a suitable proxy for estimating the BM of extinct lagomorphs ($r^2 = 0.970$, $SEE = 0.089$, $\%PE = 15.427$) (Moncunill-Solé et al., 2015, 2016a, 2021): $\log BM = 0.461 + 2.584 \log TTDd$; with a correction factor $RE = 1.013$.

The model has been developed considering extant species of lagomorphs ($N = 44$) with a worldwide distribution and covering the size diversity of the order Lagomorpha.

Terminology

In this paper, we often refer to “stem lagomorphs” and “continental Europe”. To avoid the risk of misunderstandings or oversimplifications, we consider appropriate to contextualize the usage of those terms in this paper. Further insights, discussion, and comparisons to be found in Angelone et al. (2017: p. 458).

STEM LAGOMORPHS - The early representatives of the order Lagomorpha are informally referred in literature as “stem lagomorphs”. López Martínez (2008: p. 31-32) defines stem lagomorphs as “the plesion or paraphyletic group of primitive true lagomorphs”. Thus, by definition, the group includes forms which may be very distant under a phylogenetic point of view. The term does not have a temporal sense either. In some areas, stem lagomorphs persist and coexist with representatives of crown groups for several millions of years (see section *Paludotona*, a ghost lineage represented by Late Miocene living fossils). Stem lagomorphs are characterized by some common, distinctive, archaic features which are lost in crown groups (see Angelone et al., 2017: p. 458). This said, following López Martínez (2008), in this paper the term “stem lagomorph” is used in its morphological sense, without any phylogenetical or temporal implication.

MAINLAND EUROPE/CONTINENTAL EUROPE - We mainly address two periods of time in this paper: an interval around ~8.3-6.7 Ma, in which the terms “continental Europe” or “mainland Europe” can be unequivocally used, in spite of the obvious differences between modern palaeogeography and that of ~25-22 Ma, when “Europe” consisted in a puzzle of emerged lands around a proto-Mediterranean Sea and the Paratethys (Rögl, 1998; Popov et al., 2004). MP28-MN1 stem lagomorphs are concentrated in today’s western and central Europe. It is quite possible that the ancestor of *Paludotona* lived in that region, also because the components of the early-middle Turolian Tusco-Sardinia palaeobioprovince were originally part of that landmass. For the sake of simplicity, we use here the terms “continental Europe” or “mainland Europe” to address the source of insular endemic stem lagomorphs of the Western Mediterranean.

TUSCO-SARDINIA PALAEOBIOPROVINCE - We have some glimpses of the existence of the Tusco-Sardinia palaeobioprovince only for a very short part of its existence (~8.3-6.7 Ma), but fossil lagomorphs point to a condition of isolation *sensu lato* for a time span at least ten times longer (*Paludotona*, a ghost lineage represented by Late Miocene living fossils). We have no clue of the palaeogeographical asset of the palaeobioprovince prior to ~8.3 Ma. Theoretically, it would not be correct to refer to an area of which we do not know the full extent, geographical asset, and relative position with respect to the mainland, with the same name of a known entity as the Tusco-Sardinia palaeobioprovince. However, to avoid confusion, we decided to extend the term Tusco-Sardinia palaeobioprovince to indicate also the landmass that hosted *Paludotona* and its evolution for several million years.

RESULTS

BM of *Paludotona*

Based on TTDd, which is among the most reliable BM proxies (Moncunill-Solé et al., 2015, 2016b, 2021), the specimen of *Paludotona* cf. *minor* to which pertained the tibial fragment Bac. 793 weighed ~1100 g (Tab. 1).

BM comparison with latest Oligocene-earliest Miocene species of European mainland

Based on available data (see Angelone et al., 2017), *Paludotona*’s continental ancestor was a pre-MN2 species, phylogenetically close to but less advanced than *Titanomys*. Such source species is at present unknown in the fossil record. Thus, in order to have an indication of the BM increase that the lineage culminated with *Paludotona* underwent in an insular environment, we should estimate the BM of latest Oligocene/earliest Miocene (MP28-MN1) European lagomorphs. However, when postcranial bones are available for those taxa, unequivocal attributions to species are far from certain, due to the lack of detailed studies (see Materials and methods).

The BM of the taxa selected for comparison, obtained basing on the proxy HL (Tab. 1), is estimated to ~350 g for “*Amphilagus*” *wuttkei* from Enspel (MP28), and to ~145 g for *Amphilagus* vel *Piezodus* from Rott (MP30).

	inventory number	proxy	measurement (mm)	BM (g)
<i>Paludotona cf. minor</i>	NHMB Bac. 793	TTDd	9.92	1100.51
" <i>Amphilagus</i> " <i>wuttkei</i>	NHMM/LS PW2000/5021a	HL	36.60	363.76
" <i>Amphilagus</i> " <i>vel Piezodus</i>	NHM 41089	HL	25.00	144.72

Tab. 1 - List of taxa involved in the analyses with details about specific attribution, repository number, type of postcranial measurement on which the BM estimation was based (see abbreviations for details), value (in mm) of the measurement, and BM estimations (in g).

Considering greater BM in the adult stage, we may infer that the BM range of the considered lagomorphs as adults could be ~200-400 g.

DISCUSSION AND CONCLUSIONS

Paludotona, a ghost lineage represented by Late Miocene living fossils

Fossil remains of *Paludotona* have been retrieved in the early-middle Turolian (MN11-12 and possibly earliest MN13, Late Miocene) fossil assemblages referable to local biochrons V0-V1-V2, in an area pertaining at that time to the Tusco-Sardinia insular palaeobioprovince and today corresponding to Maritime Tuscany (see Bernor et al., 2001; Benvenuti et al., 2001, 2015; Rook, 2016; Rook et al., 2000, 2011).

According to the latest taxonomic revision (Angelone et al., 2017), *Paludotona* includes the species *P. etruria* Dawson, 1959 (BV1, MN11, with an estimated age of ~8.1-7.1 Ma) and *P. minor* (BV2, MN12 and possibly earliest MN13, ~7.1-6.7 Ma). A feasible distinct species, *P. aff. minor*, has been retrieved from BV0 (MN11, ~8.3-8.1 Ma). *Paludotona cf. minor* (transition BV1/BV2), though similar in morphology and dimensions to *P. minor*, is retained as a separate taxonomic entity due to the scantiness of its dental remains. *Paludotona minor* and *P. cf. minor*, i.e., the most recent species, are not anagenetically related to *P. etruria*, suggesting a fragmentation of the Tusco-Sardinia palaeobioprovince in an archipelago (Angelone et al., 2017).

As the LAD of *Paludotona* occurred at ~6.7 Ma, *P. minor* is the last stem lagomorph which lived on the Earth. Actually, the youngest remains of *Gymnesicolagus gelaberti* Mein & Adrover, 1982 from the Balearic Islands date back to the early Tortonian (~11 Ma) (Quintana & Agustí, 2007); interestingly López Martínez (2008) reported ~7 Ma as the LAD of *Gymnesicolagus*, though with no further explanation.

The oldest fossil undoubtedly referable to Lagomorpha is recorded in the middle Eocene of central Asia (~45 Ma; López Martínez, 2008 but see Rose et al., 2008 for a report at ~53 Ma in NW India). Stem lagomorphs spread in the northern hemisphere, though with a diachronic pattern. In Europe, the stem lagomorph FO occurred in the early Oligocene (MP21, ~33 Ma; Vianey-Liaud & Lebrun, 2013), i.e., relatively late with respect to their FO in North America (~43 Ma) due to palaeogeographical reasons. Apparently, Africa was never reached by stem lagomorphs (López Martínez, 2008). It seems that the earliest dispersal of lagomorphs into Europe was not immediately followed by an adaptive radiation. The group died out or was so rare,

that its representatives are not found in the fossil record, at least at present. Stem lagomorphs start to be relatively common in the European fossil record since ~25 Ma. Evidence of dispersal(s) from Asia at this time has not been found yet, nor is there evidence of a local evolution from the older Oligocene immigrants. The geographical distribution of European stem lagomorphs remained patchy and their remains scarce compared to ochotonids/prolagids also during the Miocene. The last reliable records of a stem lagomorph in mainland Europe date back to the early MN10 of Buzhor (Moldova: Lungu, 1981; see Čermák, 2016 and Sinita & Delinschi, 2016 for age attribution), the MN10 of Soblay (France: Ménouret & Mein, 2008), and the late MN10 of Schernham bei Haag (Austria: Angelone & Veitschegger, 2015). The MN10 record of Terrassa (NW Spain) cited by Fostowicz-Frelik et al. (2012) as the LAD of the stem lagomorph *Eurolagus* is questionable, as the claim is based on a paper by Agustí & Gibert (1982) lacking figures, description, and details about repository number of the supposed stem lagomorph from Terrassa. The material is unavailable in the ICP collections and database (CA, personal observation, 2012), thus the MN10 report from Terrassa has for the moment to be considered doubtful.

The estimated age for Schernham bei Haag assemblage is ~9 Ma (Daxner-Höck & Höck, 2009), thus a gap of ~2.5 my separates the disappearance of the last stem lagomorph in continental Europe and their LAD in the Tusco-Sardinia palaeobioprovince. During the Late Miocene, then, *Paludotona* represented a living fossil.

As previously stated, *Paludotona* most probably originated from a pre-MN2 taxon (Angelone et al., 2017), thus the lineage developed in isolation sensu lato during millions of years without leaving any fossil record. *Paludotona* was a ghost taxon for at least 14 my (Fig. 2), and its fossil record (covering the last ~1.6 my of its existence) at the moment represents only ~15% or less, of the total temporal range of this insular endemic taxon. Thus, the Tusco-Sardinia palaeobioprovince served as a refugium for the last stem lagomorphs, but this is not the only example of a Western Mediterranean isolated domain representing a refugium for lagomorphs and other mammals. The classic example is the last prolagid, *Prolagus sardus* (Wagner, 1825), which continued to thrive in Sardinia and Corsica at least until the earliest phases of the Iron Age and until the Roman period respectively (Masala, 2015 with references), i.e., for ~150.000 years after the LO of the genus in continental Europe (López Martínez, 2001).

Ecological insights about the genus Paludotona

BM variations are correlated to substantial changes in several functions of an organism. In insular environments,

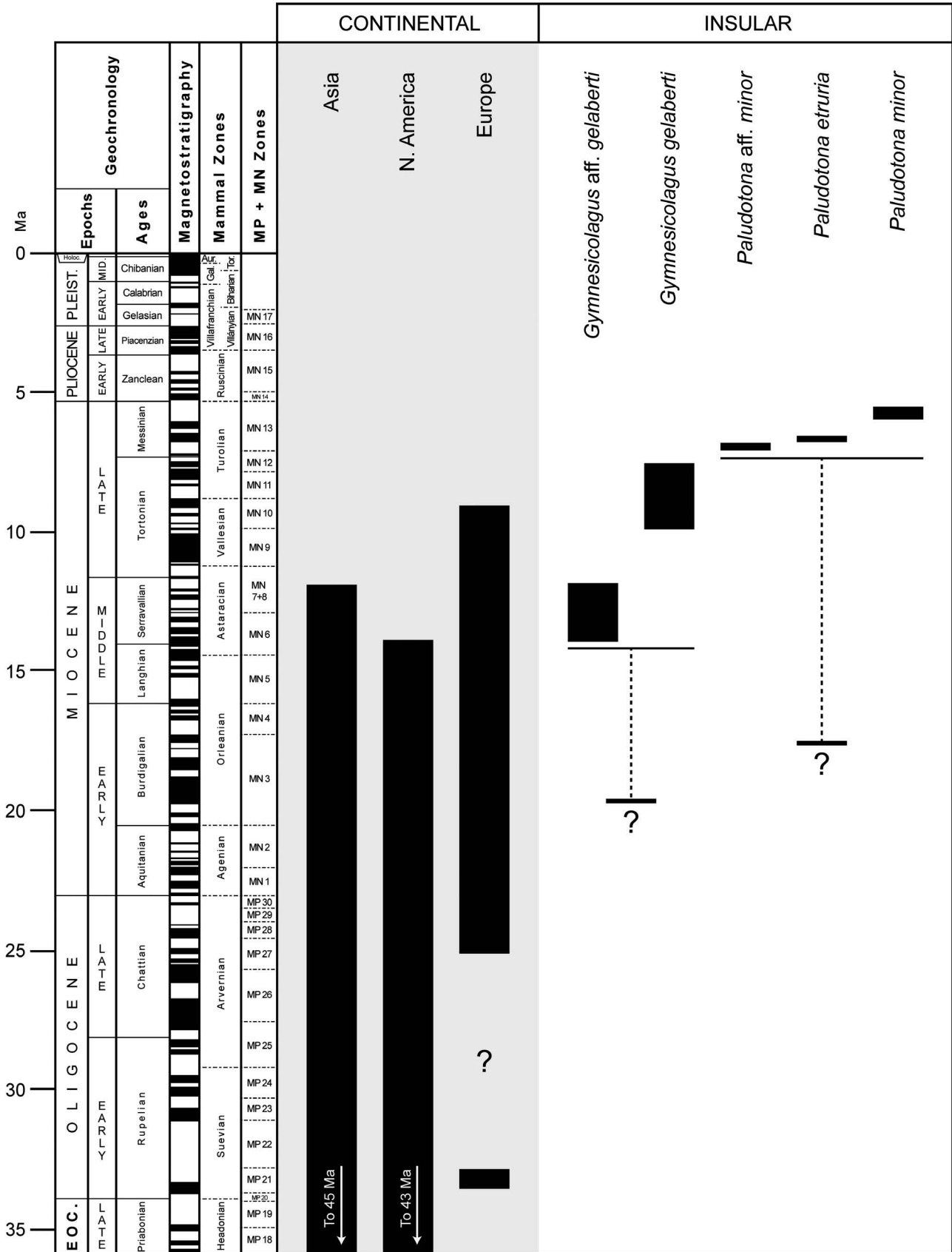


Fig. 2 - Temporal distribution of stem lagomorphs in continental Asia, North America and Europe, with emphasis on insular endemic stem lagomorphs of the Western Mediterranean islands.
 Holoc.: Holocene; Pleist.: Pleistocene; Mid.: Middle; Eoc.: Eocene; Aur.: Aurelian; Gal.: Galerian; Tor.: Toringian.

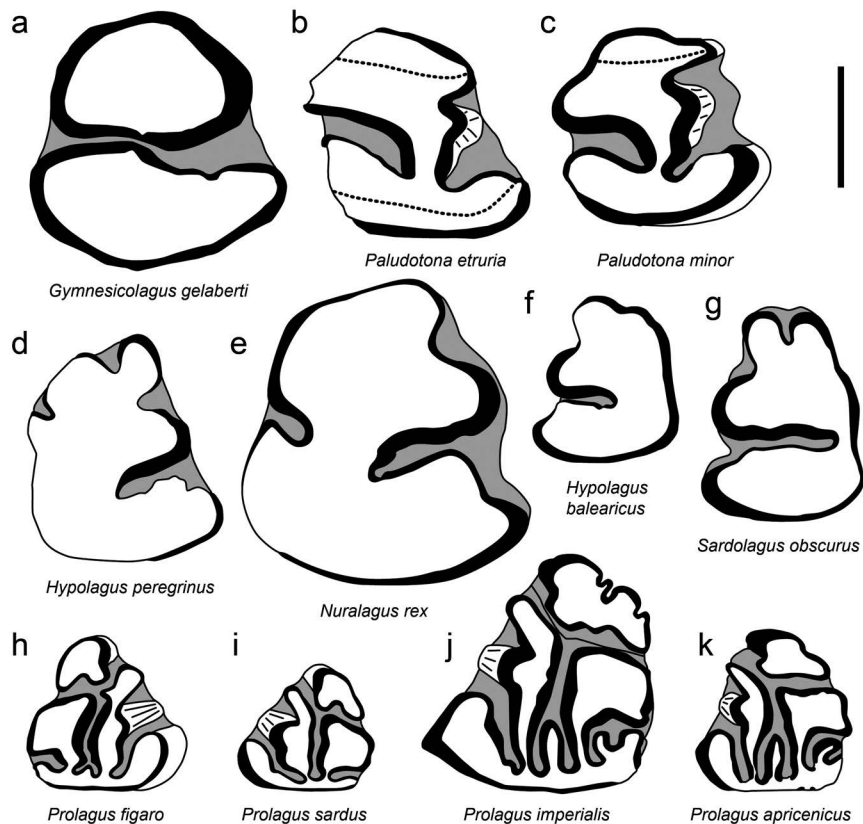


Fig. 3 - Comparisons of dental remains (lower third premolar, p3) of insular endemic lagomorphs of the Neogene Western Mediterranean. a) *Gymnesicolagus gelaberti* (Mallorca, MN5 and Menorca, early Tortonian; drawing CA pers. database). b) *Paludotona etruria* (Tuscany, BV1, MN11; Angelone et al., 2017: fig. 2C, p. 461). c) *Paludotona minor* (Tuscany, BV2, MN12-?earliest MN13; Angelone et al., 2017: fig. 2I, p. 461). d) *Hypolagus peregrinus* Fladerer & Fiore, 2003 (Sicily, late Early Pleistocene; Fladerer & Fiore, 2003: fig. 2d and 2f, p. 42). e) *Nuralagus rex* (Punta Nati-Cala's Pous, Menorca, Early Pliocene; Quintana Cardona, 2005: fig. 20b, p. 65). f) *Hypolagus balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 (Ses Fontanelles, Eivissa, Late Miocene-Early Pliocene; Bover et al., 2010: fig. 3B, p. 558) g) *Sardolagus obscurus* Angelone, Čermák, Moncunill-Solé, Quintana, Tuveri, Arca & Kotsakis, 2018 (Sardinia, ?latest Pliocene/earliest Pleistocene-late Early Pleistocene; Angelone et al., 2018: part of fig. 2.8, p. 509). h) *Prolagus figaro* López Martínez, 1975 in López Martínez & Thaler, 1975 (Sardinia, latest Pliocene/earliest Pleistocene-late Early Pleistocene; Angelone et al., 2020: fig. 11, p. 159). i) *Prolagus sardus* (Corsica and Sardinia, Middle Pleistocene-Holocene; Angelone et al., 2008: fig. 3e, p. 113). j) *Prolagus imperialis* Mazza, 1987 (Gargano palaeoarchipelago, Messinian-?earliest Pliocene; Mazza, 1987: pl. 3.4, p. 239). k) *Prolagus apricenicus* Mazza, 1987 (Gargano palaeoarchipelago, Messinian-?earliest Pliocene; Mazza, 1987: pl. 1.26, p. 235, reversed).

small mammals tend to have enlarged BM compared to their continental ancestors (see Adler & Levins, 1994 for a discussion about the “island syndrome” in insular populations of extant rodents). As for lagomorphs, there is no univocal datum regarding the BM trend followed by extant species in insular environments (see Foster, 1964; Lomolino, 1985). In the case of fossil lagomorphs, the data available for insular endemic taxa of the Neogene of the Western Mediterranean are at the moment quite incomplete and do not provide unequivocal BM trends (cfr. BM estimations in Quintana Cardona & Moncunill-Solé, 2014; Moncunill-Solé et al., 2015).

LIFESPAN - It is undeniable that *Paludotona* underwent a noticeable BM increase with respect to the continental stock from which it originated. A direct allometric relationship between BM and lifespan has been observed in extant organisms (Speakman, 2005 with references). Indeed, an increase in the lifespan of some insular endemic fossil lagomorphs (compared to the closest

living continental taxon) has been demonstrated by palaeohistological analyses (Riyahi et al., 2011; Moncunill-Solé et al., 2016a). In the case of *Paludotona*, an increased life span has already been suggested to explain some dental features (indeed very common in fossil insular endemic mammals) as high crown, loss of dental roots, extra elements of occlusal surface (Angelone et al., 2017: p. 468).

LOCOMOTORY HABITS - A side effect of BM increase may be changed locomotion. Sometimes the changes detected in insular endemic mammals of Western Mediterranean islands are explained as an adaptation to a rocky and rugged landscape, or as a consequence to the absence of terrestrial predators (because selection favors energy-saving morphologies). This may be true or quite determinant for some taxa (Moncunill-Solé, 2021), but in other cases, change in locomotion is very likely a consequence of the BM increase. The leporid *Nuralagus rex* Quintana, Köhler & Moyà-Solà, 2011

from Punta Nati-Cala's Pous, Menorca (Early Pliocene) weighed ~8000 g (Quintana et al., 2011; Moncunill-Solé et al., 2015): no wonder a plantigrade locomotion was selected. The postcranial remains of *Paludotona* presently available do not allow inference about locomotion or ecological adaptations such as cursoriality/saltatoriality/fossoriality/burrowing. The distal tibiofibular fragment of *Paludotona* cf. *minor* here studied presents an extended facet (squatting facet) of the talocrural joint in the anterior margin of distal epiphysis. This well-developed facet would be related to a prolonged contact of tibiofibula and astragalus in a dorsiflexion position. For leporids, its presence has been associated to the resting crouched plantigrade standing and digitigrade posture during locomotion (Best, 1996; Dunn & Rasmussen, 2009). It also functions in leaping mechanics, which require that individuals crouch (flexion of talocrural joint) before extending hindlimbs (Godinot & Dagosto, 1983). In this regard, the appearance and development of this trait is functionally ambiguous, as it is observed in vertical clinging and leaping primates, plantigrade hedgehogs and tenrecs, and leaping macroscelideans (Dunn & Rasmussen, 2009 and references therein). The absence of tarsal remains of *Paludotona* prevents us from identifying corresponding facets on the astragalus for further insights in locomotor significance.

SYNECOLOGICAL CONSIDERATIONS - The evolutionary drivers of the increase of the BM of small mammals in insular environments may be several and interdependent. According to some authors the absence of terrestrial predators is among the primary ones: directly by release of predation pressure (ecological hypothesis) or indirectly by lower extrinsic mortality (life history hypothesis). Indeed, in terrestrial insular environments, carnivores are less diverse than in balanced, continental assemblages, or sometimes completely absent as in the case of the BV0-BV1-BV2 assemblages, in which there is evidence of lutrines but not of terrestrial carnivores (Rook et al., 1999). This condition is frequent in Western Mediterranean insular endemic environments (e.g., Terre Rosse faunal

assemblage of the Gargano palaeoarchipelago; Masini et al., 2010).

An insular endemic giant

Paludotona has been considered a quite large animal basing on the size of its teeth and jaws since its discovery. Dawson (1967) defined *Paludotona* as "a large ochotonid allied to the line of *Lagopsis*" Schlosser, 1884. Dawson's (1967) phylogenetic considerations about *Paludotona* do not match recent studies, in which a possible relationship with *Lagopsis* and ochotonids in general is discarded (see Angelone et al., 2017). However, it is a fact that the teeth of *Paludotona* are quite large compared to any other European lagomorph, even when compared to those of most insular endemic species of lagomorphs (Fig. 3). Actually, the differential diagnosis of *Paludotona* states (Angelone et al., 2017: p. 459): "The p3 of *Paludotona* is the largest among European ochotonids and stem lagomorphs except for *Prolagus imperialis* Mazza, 1987 and *Gymnesicolagus gelaberti* Mein & Adrover, 1982".

Recent studies quantitatively demonstrated how, in the case of extinct lagomorphs, teeth dimensions may sometimes provide results of BM estimation that are not in line with estimations based on postcranial bones (Moncunill-Solé et al., 2016b, 2021). Actually, large-toothed species may have a smaller BM than species with smaller teeth. An emblematic example is the anagenetic insular endemic lineage of Sardinian *Prolagus*. The latest Pliocene/earliest Pleistocene-late Early Pleistocene species *P. figaro* has a quite large p3, while its descendant *P. sardus* (Middle Pleistocene-Holocene) has a smaller p3, especially in the earliest populations; yet BM of *P. figaro* is less than that of *P. sardus* (Moncunill-Solé et al., 2016a).

Nevertheless, BM estimation of *Paludotona* cf. *minor* confirms the impression given by its teeth: this taxon is a real giant, when we consider that the BM of the taxa of the continental stock from where it originated should have been around 200-400 g (see section *BM comparison with latest Oligocene-earliest Miocene species of European mainland*, and Fig. 4).

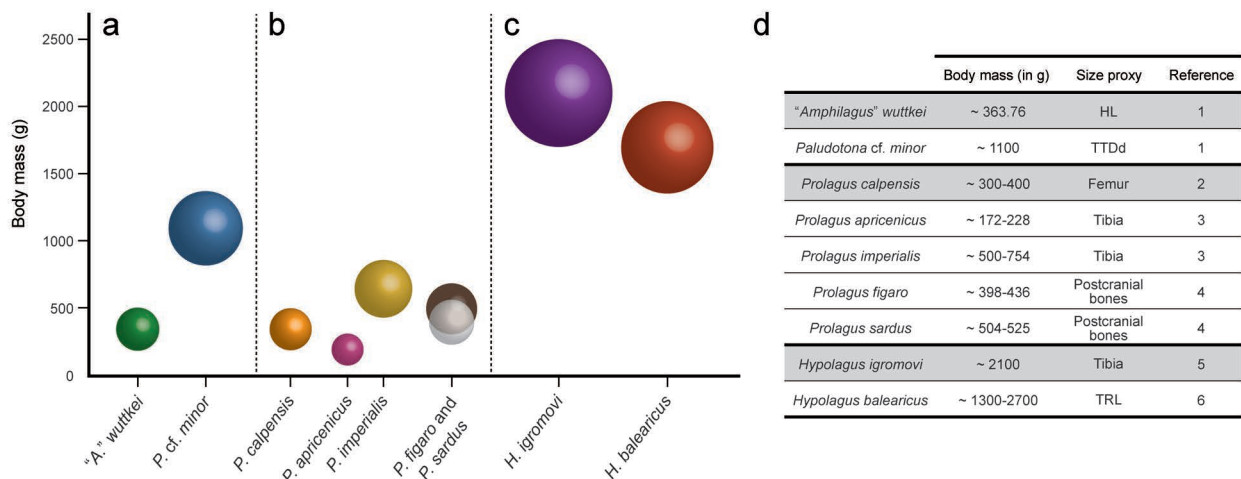


Fig. 4 - (color online) Approximate proportional size increase between some selected insular endemic lagomorphs of the Western Mediterranean and related continental taxa. These latter are not the direct ancestors of insular endemics, but represent the closer continental taxa for which a BM estimation is available.

Why so big?

Among the two known genera of stem lagomorphs which developed in an insular environment, *Paludotona* is the only one for which is available an indicative BM increase with respect to the continental stock (approximated to 3 to 5 times: ~1100 g vs ~200-400 g; Fig. 4).

Is BM increase evidenced in *Paludotona* related to the time spent in an insular domain? The examples of living insular endemic taxa analyzed by López Martínez (2001: p. 228) demonstrate that there is no positive and univocal correlation between the time spent in an isolated domain and the entity of morphological modifications, at least in lagomorphs. Trying to unravel the time/morphological change issue in the case of *Paludotona* is nevertheless impossible at the moment as we do not actually know how many million years of isolation the lineage actually spent in an insular domain. The fact that the origins of *Paludotona* date back to MP28-MN1 attests for an isolation of the area sensu lato, not necessarily for the existence of an insular domain sensu stricto. According to Mein's biphasic model (1983; see also Millien, 2006), the main morphological and dimensional changes observed in mammal species in insular environments are rapid and occur immediately after the onset of isolation, followed by a subsequent stasis. However, Moncunill-Solé et al. (2016b) discussed one case in which a taxon underwent for a second time significant and sudden morpho-dimensional changes along the lines of Mein's model, well after its arrival on the island, in correspondence of a climatic/ecological shift (see also Cucchi et al., 2014; Moncunill-Solé et al., 2016c).

In the case of *Paludotona*, indeed several ecological changes occurred along its long evolutionary history, lasted at least 14 my through almost all the Miocene, and possibly also through the last part of the Oligocene. Such changes were driven by a plethora of different biotic and abiotic factors and by the interactions among them, triggering each time new pulses of rapid evolution. The main ones can be the following, though their relative importance, in absolute terms and through time cannot be assessed:

1. Global climate change; several climatic shifts occurred during the Miocene, but it is not possible at present to discuss particular influences on the *Paludotona* lineage as we have a very limited record of fossils.

2. Changes in faunal assemblages caused for example by interactions with mainland taxa; one occurred at ~8.3-8.1 Ma, attested by the presence in the BV0 assemblage of an European murid (Rook et al., 1999 and references therein).

3. Changes in palaeogeography; the area of an insular domain, subject to changes through time due to eustatic and/or tectonic factors, strongly influences the BM in insular environments, especially as far as small mammals are concerned (Lomolino et al., 2013). In our opinion, though, also the fragmentation of the area of the insular domain has an impact on BM. Indeed, Li et al. (2021) noticed in extant species a correlation between body size enlargement and fragmentation of the original distribution area (see also Schmidt & Janssen, 2003). In the case of the Tusco-Sardinia palaeobioprovince, the area was fragmented in an archipelago, and the arrangement and the area of the islands and the connections among

them evidently changed through time (Angelone et al., 2017).

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