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# Systematics and paleobiogeography of *Sardolagus obscurus* n. gen. n. sp. (Leporidae, Lagomorpha) from the early Pleistocene of Sardinia

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**Abstract.**—The extreme rareness of Sardinian fossil sites older than Middle and Late Pleistocene makes the Monte Tuttavista karst complex (E Sardinia, Italy) very important. Remarkable lagomorph material, recovered from several fissure infillings of Monte Tuttavista referable to the Capo Figari/Orosei 1 and Orosei 2 faunal sub-complexes (early Pleistocene, ~2.1/1.9–1.1 Ma), allowed us to describe a new endemic insular leporid, *Sardolagus obscurus* n. gen. n. sp. The new taxon is characterized by a peculiar combination of an advanced p3 (*Lepus*-type) and a primitive P2 lacking deep flexa. The origin of such discrepancy, unprecedented among continental and insular endemic European leporids, is unclear. It could be the result of: (1) an independent evolution of p3 from an ancestor bearing the primitive P2/p3 (e.g., *Alilepus*, *Hypolagus*), or (2) a selective reversal morphocline from an *Oryctolagus*/*Lepus*-like leporine. The lack of data about the phylogenetic origin of the new taxon makes any inference about its possible arrival to Sardinia problematic. Crossing the European leporid records and evidence of migrations to Sardinia, we hypothesize three possible ages in which the ancestor of *Sardolagus obscurus* could have arrived in Sardinia, restricted to the late Miocene–early/late Pliocene (~8–3.6 Ma). The phylogenetic relationship between *Sardolagus obscurus* n. gen. n. sp. and the oldest Sardinian leporid, recorded from Capo Mannu D1 and dated at the early/late Pliocene boundary (~3.6 Ma), is unclear at present, however it is quite likely that they pertain to the same lineage.

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## Introduction

The first overviews of the Monte Tuttavista fossiliferous karst complex date back to the early years of the twenty-first century (Rook et al., 2003; Abbazzi et al., 2004). Discovery of the Monte Tuttavista karst complex (E Sardinia, Italy) (Fig. 1) was extremely important for understanding the paleobiological history of Sardinia because of the extreme abundance of vertebrate fossil material, a very high taxonomical diversity, but mainly the time span covered (early Pleistocene to Holocene). Actually, fossil sites older than Late Pleistocene are rare in Sardinia and Corsica. Discovery of the Monte Tuttavista fossil assemblages provides a remarkably deeper insight of the Quaternary fauna of Sardinia. Several species noted in the Monte Tuttavista fissure fillings have been reported for the first time in Sardinia. As far as lagomorphs are concerned, the Monte Tuttavista quarries provided remarkable material for the study of insular endemic Sardinian ochotonids (Angelone et al., 2008), and led to the discovery of the remains of a new early Pleistocene leporid. This leporid was first reported and preliminarily classified in Rook et al. (2003) and Abbazzi et al. (2004) as *Oryctolagus* aff. *O. lacosti*. Detailed studies of the original material and of recent findings allowed us to erect a new leporid taxon, *Sardolagus obscurus* n. gen. n. sp., here described in the framework of coeval peri-Mediterranean leporids.

## Materials and methods

Dental terminology, metrics, and morphotype classification used to describe teeth follow Sych (1965), Palacios and López Martínez (1980), Fladerer (1987), Fladerer and Reiner (1996), and Čermák et al. (2015). The original scheme of P2 morphotypes by Fladerer and Reiner (1996), originally used for *Hypolagus*, was extended here by adding the BMR-morphotype "C" (characterized by very long hypoflexus) in order to be applicable also to advanced/modern taxa of Leporidae. For a quantification of degree of P2 complexity, we assigned to the morphological classes I → II → III → IV → V → VI of the LL-morphotype and to the classes 0 → A → B → C of the BMR-morphotype the nominal values 1–2–3–4–5–6 and 1–2–3–4, respectively,

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* corresponding author

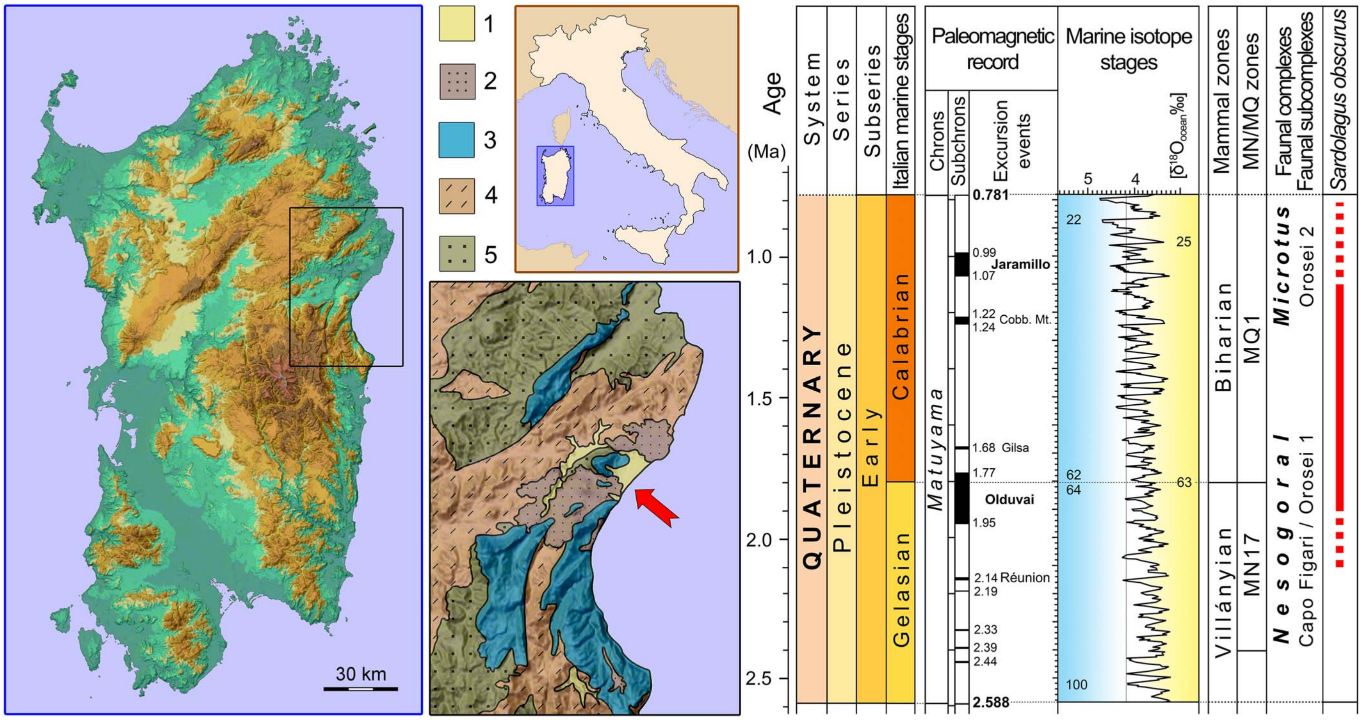

**Figure 1.** Geographical location of Monte Tuttavista and age span of *Sardolagus obscurus* n. gen. n. sp. Legend of lithology: (**1**) Quaternary deposits; (**2**) Pliocene within-plate basalts; (**3**) Permian to early Eocene volcano-sedimentary rocks; (**4**) late Variscan magmatic complex; (**5**) Variscan metamorphic basement (modified from Carmignani et al., 2016).

indicating the number of evolutionary steps. The quantification of P2 complexity is given by the sum of nominal values of assigned LL- and BMR-morphotypes. Drawings and measurements of teeth were made using a camera lucida and an ocular micrometer on a binocular microscope. Measurements of cranial and postcranial elements were made using a digital caliper (error: 0.05 mm). All length dimensions are given in millimeters (mm) and weight estimates in grams (g). We reserve the formal term 'crown Leporinae' for the group of extant hares and rabbits; the formal term 'Leporinae', or informally 'leporines', for the leporid group, including *Alilepus* Dice, 1931 and presumed descendants; and fossil genera closely related to that radiation are 'stem Leporidae' or informally 'modern leporids' (Flynn et al., 2014; Čermák et al., 2015). For geologically older genera distantly related to the modern radiation, we informally use the term 'leporid,' or simply 'lagomorph.' Biostratigraphic terminology follows Palombo (2009). All nomenclatural acts presented here conform to the mandatory provisions of the International Code of Zoological Nomenclature (ICZN, 1999). Country abbreviations follow ISO 3166-1 alpha-2 codes.

We analyzed samples from Monte Tuttavista fissure fillings VIIbs, X4, and part of the material from IVm. Because our preliminary analyses did not show taxonomic differences between the leporid samples extracted from different karst fissures, we analyzed the material in its entirety. For taxonomic considerations, we used dental and cranial material; for BM estimation the postcranial one. We followed the methodology for BM estimation described and illustrated by Moncunill-Solé et al. (2015, fig. 1). Due to the poor number of postcranial specimens, only the following measurements were taken on this new species of leporid: femur length, proximal femoral transversal diameter, distal femoral anteroposterior diameter, distal femoral transversal diameter, distal humeral anteroposterior diameter, distal humeral transversal diameter, proximal tibia anteroposterior diameter, proximal tibia transversal diameter, and distal tibia transversal diameter. Once the BM was obtained for each specimen, we calculated an arithmetic mean and a confidence interval for each specific measurement. Finally, we performed an arithmetic average to estimate the weight of the species.

*Repositories and taxa under comparison*.—The material is curated in the Laboratorio di Paleontologia, Dipartimento di Scienze, Università Roma Tre (Italy). The interspecific comparisons were made with the following taxa, based on original material (indicated by "*") or on a bibliographical basis (unless otherwise stated, data were taken from the original descriptions of species):

**Alilepus laskarewi* (Khomenko, 1914) from Tarakliya (type locality) (MD), Chimishliya (MD), and Egorovka 2 (UA)—late Miocene (middle Turolian, MN 12); collections: National Museum of Natural History, V. Topachevsky Paleontological Museum (Kiev); Odessa I.I. Mechnikov National University, Paleontological Museum; National Museum of Ethnography and Natural History (Kishinev).

*Alilepus turolensis* López Martínez, 1977 from El Arquillo (type locality) (ES)—late Miocene (late Turolian, MN13).

**Alilepus meini* Angelone and Rook, 2011 from Ribardella (type locality) (I)—late Miocene (late Turolian, MN13); collections: "Museo di Storia Naturale" (Geology and Palaeontology Section) at the University of Florence.

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**Nuralagus rex* Quintana et al., 2011 from Punta Nati 6 (type locality) (ES, Minorca)—late Neogene (post-Messinian, Pliocene); collections: Museu de l'Institut Català de Paleontologia Miquel Crusafont (Sabadell).

*Hypolagus peregrinus* Fladerer and Fiore, 2003 from Monte Pellegrino (type locality) (I, Sicily)—early Pleistocene.

**Hypolagus petenyii* Čermák and Fladerer in Čermák, 2009 from Hosťovce 2 (SK), Ivanovce 1 (SK), Měňany 3 (CZ)—Pliocene (late Ruscinian–early Villányian, MN 15b–16a); collections: temporarily in the Institute of Geology of the Czech Academy of Sciences (Prague).

**Hypolagus brachygnathus* (Kormos, 1930) from Chlum 4, 6, 8 (CZ), Gombasek (SK), Holštejn (CZ), Lažánky 2 (CZ), Mladeč 3–point [7/10] (CZ), Stránská skála (CZ) and Včeláre 4E, 6/8 (SK)—early Pleistocene (Biharian); collections: temporarily in the Institute of Geology of the Czech Academy of Sciences (Prague).

**Hypolagus balearicus* Quintana et al., 2010 from Caló d'en Rafelino (type locality) (ES, Mallorca)—earliest Pliocene?; collections: Institut Mediterrani d'Estudis Avançats (Esporles).

*Serengetilagus tchadensis* López Martínez et al., 2007 from Toros Menalla (type locality) (TD)—late Miocene.

**Serengetilagus praecapensis* Dietrich, 1941 from Laetoli (TA)—Pliocene; collections: Museum für Naturkunde (Berlin).

**Pliopentalagus dietrichi* (Fejfar, 1961) from Ivanovce (*type locality) (SK), Muselievo (BG), and Budăi (MD) (see Čermák and Wagner, 2013 for details)—early Pliocene (late Ruscinian, MN15b).

*Pliopentalagus huainanensis* Jin, 2004 from Laodong cave (type locality) (CN)—late Miocene.

*Pliopentalagus dajushanensis* Tomida and Jin, 2009 from Xindong cave (type locality) (CN)—early Pliocene.

*Pliopentalagus anhuiensis* Tomida and Jin, 2009 from Tiesiju cave (type locality) (CN)—late Pliocene.

*Trischizolagus crusafonti* (Janvier and Montenat, 1971) from La Alberca (type locality) (ES)—late Miocene (MN13).

*Trischizolagus maritsae* De Bruijn et al., 1970 from Maritsa (GR, Rhodes)—late Miocene/?early Pliocene (MN 13/?14).

*Trischizolagus dumitrescuae* Radulesco and Samson, 1967 from Măluşteni (type locality) (RO) and Bereşti (RO)—early Pliocene (MN14b–15a). Supplementary, still unpublished material of *Trischizolagus* from other Pliocene localities is tentatively referred to as *Trischizolagus* sp. (Čermák, unpublished data).

*Oryctolagus laynensis* López Martínez, 1977 from Layna (ES)—early Pliocene (MN15).

**Oryctolagus valdarnensis* (Weithofer, 1889) from Valdarno (type locality) (I) and Pirro Nord (I)—early Pleistocene; collections: Basel Naturhistorisches Museum; "Museo di Storia Naturale" (Geology and Palaeontology Section) at the University of Florence.

*Oryctolagus giberti* De Marfà, 2008 from Cueva Victoria (type locality) (ES)—early Pleistocene.

*Oryctolagus lacosti* (Pomel, 1853) from Perrier-Étouaries (type locality) (FR), Saint Vallier (FR), and El Carmel (ES)—early–Middle Pleistocene (MN17–MQ2); data taken from López Martínez (1989), De Marfà (2009), and De Marfà and Mein (2007).

*Oryctolagus burgi* Nocchi and Sala, 1997 from Grotta Valdemino (type locality) (I), data taken from De Marfà (2009)—Middle Pleistocene.

**Oryctolagus cuniculus* (Linnaeus, 1758); recent populations of Central Europe; collections: National museum (Prague).

**Lepus europaeus* Pallas, 1778; recent populations of Central and Eastern Europe; collections: National museum (Prague), Zoological Institute, Russian Academy of Sciences (Saint Petersburg).

**Lepus timidus* Linnaeus, 1758; recent populations of Northern Europe; collections: Museum für Naturkunde (Berlin).

*Abbreviations*.—IVm = fissure filling IV *Macaca*; VIIbs = fissure filling VII blocco strada; X4 = fissure filling X4; BM = body mass; FAD = first appearance datum; FC = Faunal Complex; FSC = faunal subcomplex; IC = confidence interval; N = number of specimens; OR = observed range; x̄ = arithmetic mean.

## Systematic paleontology

*Anatomical and dimensional abbreviations*.—BMR = buccal mesial reentrant (mesoflexus) of P2; I/i = upper and lower incisors; L = length; LL = lingual lobe (hypercone) of P2; M/m = upper and lower molars; P/p = upper and lower premolars; W = width.

Order Lagomorpha Brandt, 1855
Family Leporidae Fischer, 1817

Genus *Sardolagus* new genus

*Type species*.—*Sardolagus obscurus* new species.

*Diagnosis*.—As for type species by monotypy.

*Etymology*.—After Sardinia, the location region.

*Occurrence*.—As for type species.

*Remarks*.—The Sardinian leporid shows some peculiar characters, mainly the discrepancy in p3 and P2 evolutionary stages. The combination of advanced and primitive morphotypes in upper and lower tooth rows is not a novelty in lagomorph evolution, however, in the case of the Sardinian leporid, the difference is very marked and the combination unique among leporines. Such combination is not compatible with any known genus and justifies ascription of the Sardinian leporid to a new genus.

*Sardolagus obscurus* new species
Figures 2–7, Tables 1–3

2003 *Oryctolagus* aff. *O. lacosti* (Pomel); Rook et al., p. 25, tab. 11.
2004 *Oryctolagus* aff. *O. lacosti* (Pomel); Abbazzi et al., p. 693, fig. 9, fig. 16, tab. 4.
2005 Leporidae; Palombo et al., p. 225.
2006 *Oryctolagus* aff. *O. lacosti* (Pomel); Palombo, p. 51, fig. 2.
2008 Leporidae n. gen. n. sp.; Palombo, p. 45, tab. 2.
2008 Leporidae n. gen. n. sp.; Palombo et al., p. 80.

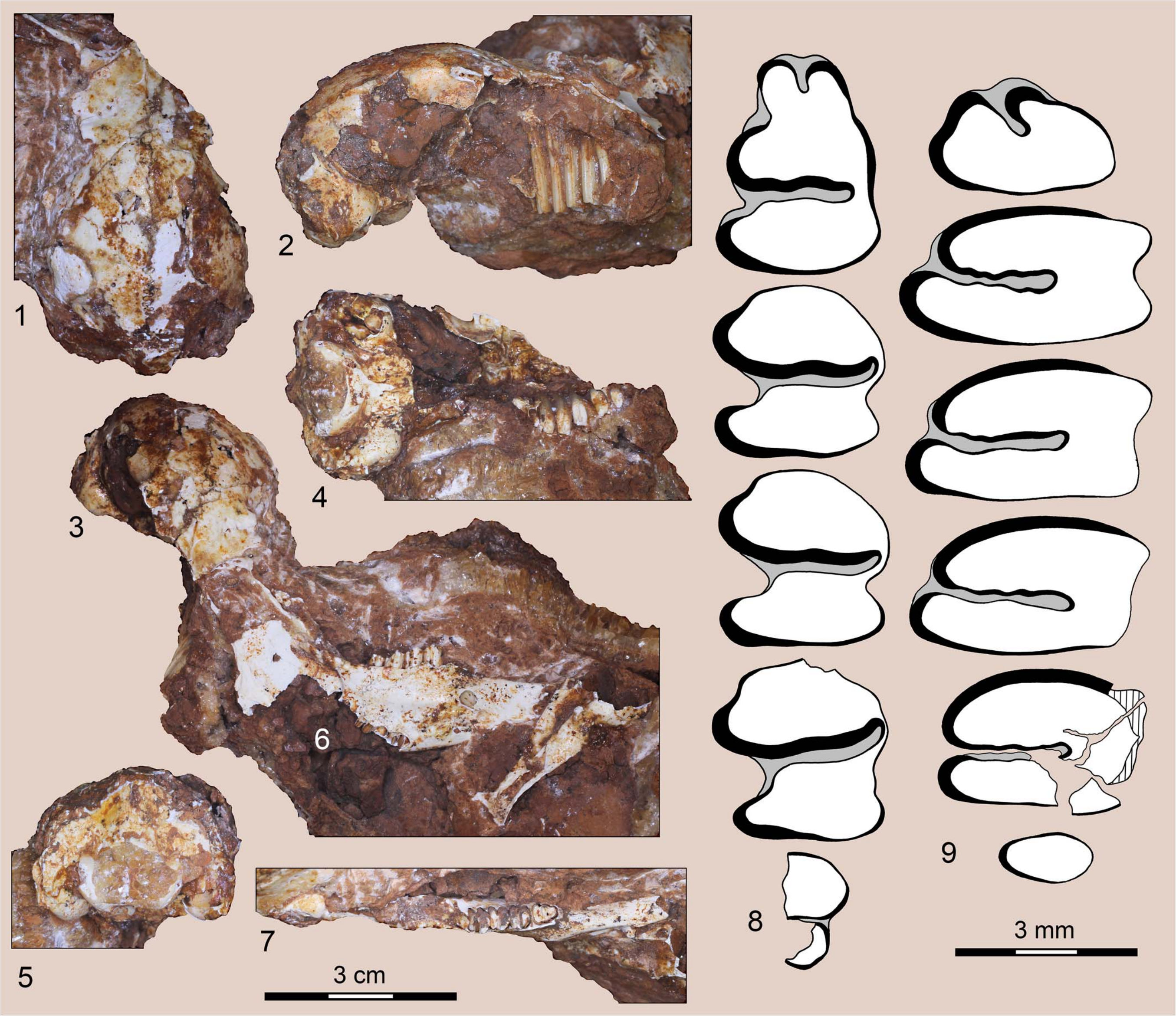

**Figure 2.** *Sardolagus obscurus* n. gen. n. sp. (**1–5, 9**) paratype (DSG/URT-053/504), incomplete cranium with left P2-M3 (**9**) in dorsal (**1**), lateral (**2**), rostral (**3**), ventral (**4**), and caudal (**5**) views; (**6–8**) holotype (DSG/URT-053/503), left incomplete hemimandible with p3-m3 (**8**) in lingual (**6**) and dorsal (**7**) views.

| | |
|---|---|
| 2009 | Leporidae n. gen. n. sp.; Palombo, p. 369, fig. 2. |
| 2010 | *Oryctolagus* n. sp.; Angelone et al., p. 5. |
| 2014 | Leporidae n. gen. n. sp.; Palombo and Rozzi, p. 140, fig. 3. |
| 2015 | cf. *Oryctolagus* aff. *lacosti* (Pomel); Angelone et al. p. 293. |

*Holotype*.—Left incomplete hemimandible with p3-m3 (Fig. 2.6–2.8), DSG/URT-053/503; early Pleistocene, MN17 (Capo Figari/Orosei 1 FSC of the *Nesogoral* FC); Monte Tuttavista VIIbs (Orosei, E Sardinia, Italy).

*Paratype*.—Incomplete cranium with left P2-M3 (Fig. 2.1–2.5, 2.9), DSG/URT-053/504; early Pleistocene, MN17 (Capo Figari/Orosei 1 FSC of the *Nesogoral* FC); Monte Tuttavista VIIbs (Orosei, E Sardinia, Italy). The cranium is associated with the holotype in a block of breccia, and they probably belong to one individual.

*Diagnosis*.—Small-sized leporid with the following features: simple P2 without or with incipient hypoflexus (prevailing LL-morphotype I) and very shallow mesoflexus (prevailing BMR-morphotype A); significantly elongated p3 with exclusively of A1/PR3 morphotype, p3 hypoflexid short (within A1/PR3; ~70–90% of W) with feeble or missing anterior tip and gradual transition from thick to thin enamel in its lingual end, p3 anteroconid morphologically variable with anteroflexid of variable depth (~5–20% of total L); I1/i1 markedly flattened anteroposteriorly; anterior and anterobuccal walls of p3-m2 talonids smooth; p4-m2 trigonid without anteroexternal reentrant; mandibular body and ramus robust, diastema relatively short, of almost the same length as the alveolar row of p3-m3; root end of lower incisor reaching the posterior part of p3; P3-M2 hypoflexus quite short (~70% of W), generally smooth.

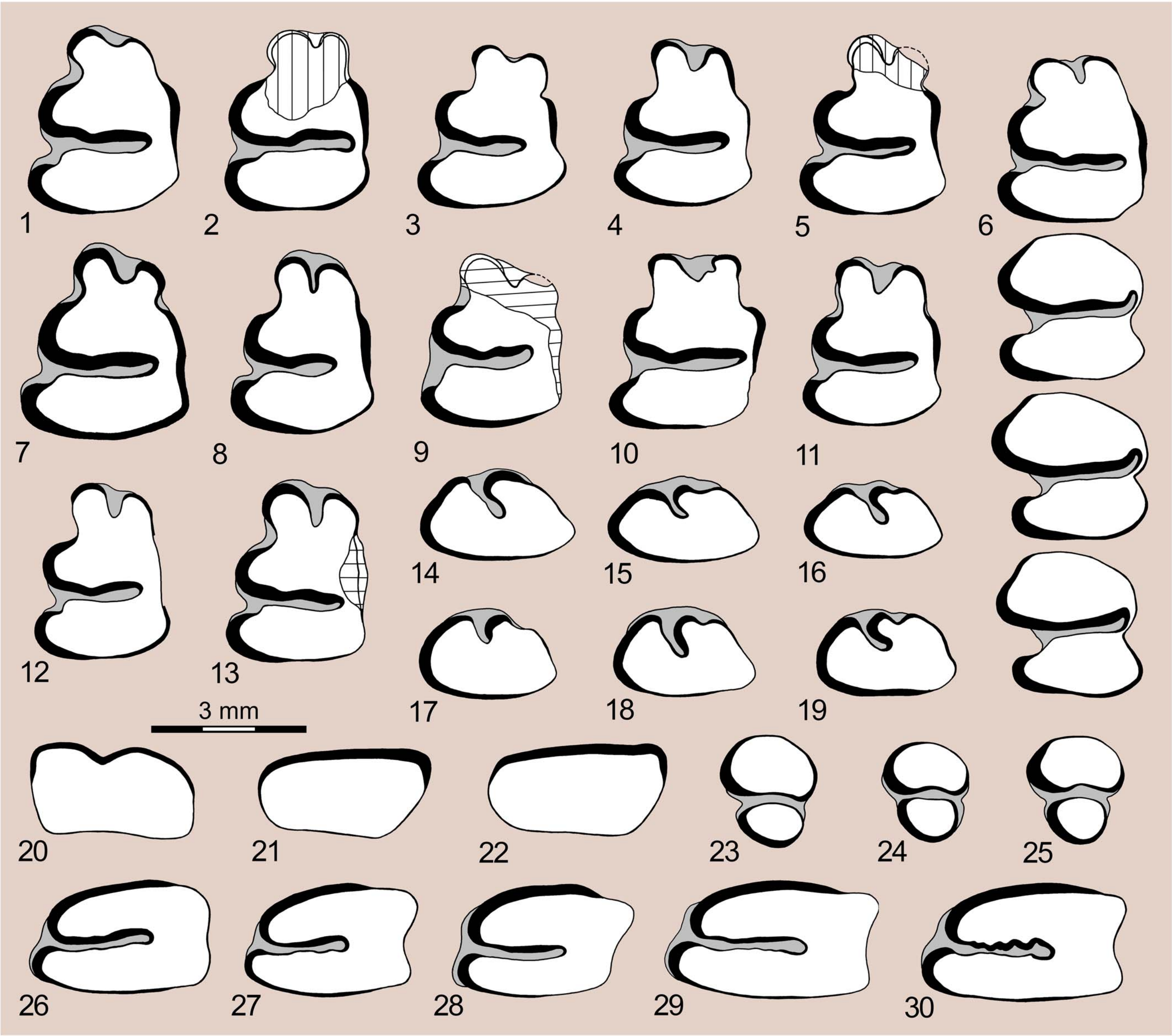

**Figure 3.** Occlusal morphology of teeth in *Sardolagus obscurus* n. gen. n. sp. (**1**) left p3, DSG/URT-053/474; (**2**) left p3, DSG/URT-053/495; (**3**) right p3, DSG/URT-053/420, reversed; (**4**) left p3, DSG/URT-053/422; (**5**) left p3, DSG/URT-053/424; (**6**) left tooth row p3-m2, DSG/URT-053/476; (**7**) right p3, DSG/URT-053/418, reversed; (**8**) left p3, DSG/URT-053/423; (**9**) left p3, DSG/URT-053/481; (**10**) right p3, DSG/URT-053/421, reversed; (**11**) right p3, DSG/URT-053/419, reversed; (**12**) left p3, DSG/URT-053/494; (**13**) left p3, DSG/URT-053/475; (**14**) right P2, DSG/URT-053/498, reversed; (**15**) right P2, DSG/URT-053/429, reversed; (**16**) left P2, DSG/URT-053/425; (**17**) left P2, DSG/URT-053/426; (**18**) left P2, DSG/URT-053/428; (**19**) left P2, DSG/URT-053/427; (**20**) right I1, DSG/URT-053/487, reversed; (**21**) left i1, DSG/URT-053/481; (**22**) left i1, DSG/URT-053/482; (**23**) left m3, DSG/URT-053/488; (**24**) left m3, DSG/URT-053/489; (**25**) left m3, DSG/URT-053/490; (**26**) right P3, DSG/URT-053/492, reversed; (**27**) right P4, DSG/URT-053/492, reversed; (**28**) right M2, DSG/URT-053/447, reversed; (**29**) right upper molariform, DSG/URT-053/500, reversed; (**30**) left upper molariform, DSG/URT-053/441.

*Differential diagnosis*.—The combination of advanced p3 (A1/PR3) and primitive P2 (absent/incipient hypoflexus, shallow mesoflexus) discriminates *Sardolagus obscurus* n. gen. n. sp. from the Old World: (1) species of *Hypolagus* bearing p3 with A0/PR0 + P2 with absent–medium hypoflexus and incipient–medium mesoflexus; (2) species of *Serengetilagus* bearing p3 with A0–1/PR0 + P2 with incipient–deep hypoflexus and shallow/medium mesoflexus; (3) *Nuralagus rex* bearing p3 with A0/PR0–1 + P2 with absent hypoflexus and incipient/shallow mesoflexus; (4) species of *Alilepus* bearing p3 with A0/PR1–2 + P2 with absent/shallow hypoflexus and mesoflexus; (5) species of *Pliopentalagus* bearing p3 with A1/PR1–2 + P2 with medium/deep hypoflexus and mesoflexus; (6) species of *Trischizolagus* bearing p3 with A0–1/PR0–1–2 + P2 with medium/deep hypoflexus and mesoflexus; and (7) species of *Lepus* and *Oryctolagus* bearing p3 with A1/PR3 + P2 with medium/deep hypoflexus and mesoflexus.

*Occurrence*.—Sardinia (Italy), Monte Tuttavista fissure fillings X4, IVm, and VIIbs; early Pleistocene, MN17–MQ1, Capo Figari/Orosei 1 FSC of the *Nesogoral* FC and Orosei 2 FSC of the *Microtus* (*Tyrrhenicola*) FC.

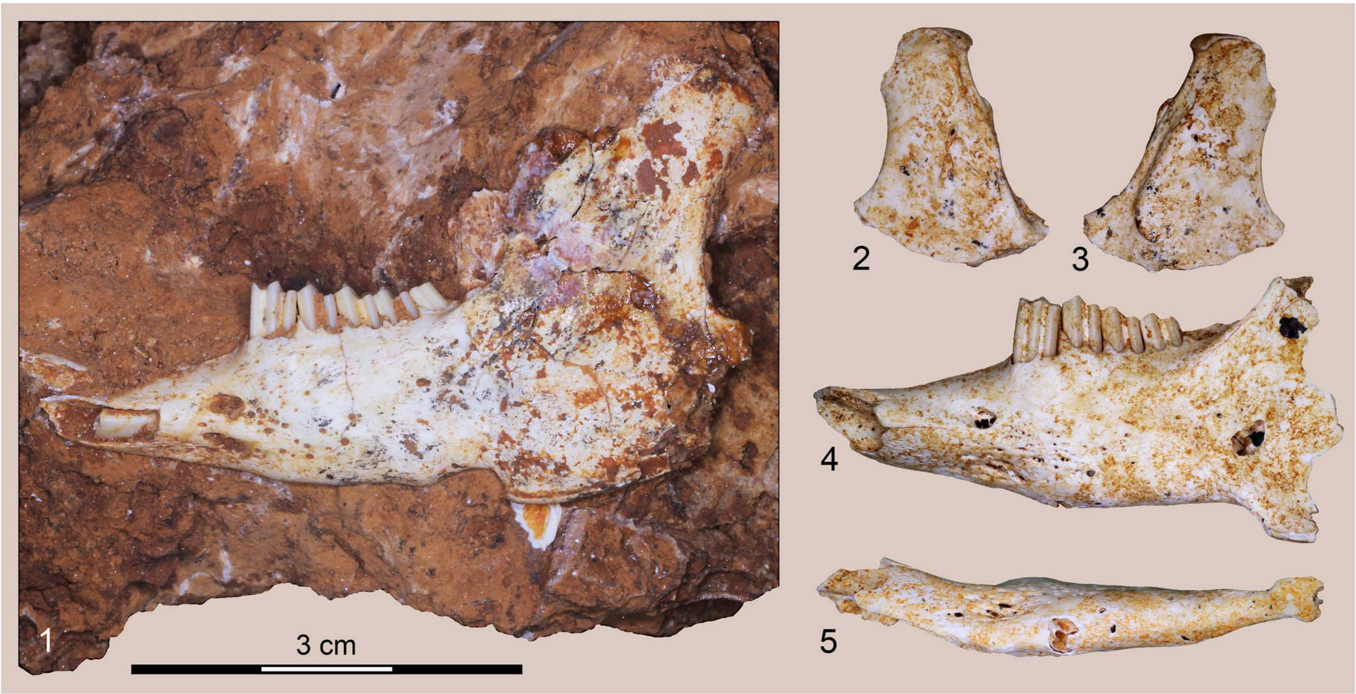

**Figure 4.** Mandibles of *Sardolagus obscurus* n. gen. n. sp. (**1**) Left hemimandible with i1, p3-m3 (DSG/URT-053/505) in buccal view; (**2, 3**) right mandibular ramus (DSG/URT-053/479) in lateral and medial views, respectively; (**4, 5**) left hemimandible with p3-m2 (DSG/URT-053/476) in buccal and ventral views, respectively.

*Description*.—We based the taxonomic analyses on isolated teeth, a few mandibular/maxillary fragments, and one incomplete cranium. Dental measurements are given in Table 1, mandibular and cranial measurements in Table 2.

Cranium (Fig. 2.1–2.5).—An incomplete cranium lacking its right lateral portion (jugale [zygomatic arch], squamosal, alisphenoid), rostrum (premaxillae, nasals, right maxilla), palatine bones, pterygoid, and basisphenoid. Parietals and frontals largely preserved, the latter lacking contact with nasals; skull roof convex; dorsal sutures well preserved, not ossified—sagittal and frontoparietal ones corrugated, the latter of "type 4" (sensu Palacios, 1989); unfused interparietal present but not well preserved; occipital condyle small; auditory bullae relatively large.

I1 (Fig. 3.20).—Anteroposteriorly flattened, roughly rectangular shape, anterior enamel of moderate thickness with no substantial variation; anterior notch shallow, V-shaped with widely opened walls, not filled with cement, dividing the tooth in two parts of approximately equal anterior prominence, the internal one (~43% of W) anteriorly flattened and rather symmetrical with respect to its anteroposterior axis, in contrast to the curved and asymmetrical external one.

P2 (Figs. 2.9 [in part], 3.14–3.19).—Simple hypercone, relatively narrow and anteriorly tapered, without or with incipient hypoflexus, LL-morphotype I (sensu Fladerer and Reiner, 1996) dominant (I: 57%, II: 29%, III: 14%, IV, V, and VI: 0%; N = 7). Lagicone with shallow mesoflexus, BMR-morphotype A (sensu Fladerer and Reiner, 1996) dominant (A: 86%, B: 14%; BMR-morphotype 0: not observed; N = 7). Simple paraflexus with variable length (very short in 2 cases). Enamel quite thick on anterior and lingual parts.

Upper molariforms (Figs. 2.9 [in part], 3.26–3.30).—Narrow teeth (low W values); relative length of mesial and distal hyperlophs variable; quite short hypoflexus (71% of W; N = 35), usually very slightly undulated or smooth. Abundant cement at the lingual end of the hypoflexus. Thick enamel on the anterior part of the mesial hyperloph and the lingual tips of hypercones; the thickness of enamel in the anterior part of the hypoflexus is variable. Differences in enamel thickness do not depend on tooth positions.

Mandible (Figs. 2.6, 2.7, 4).—Mandibular body and ramus robust; diastema relatively short, of almost the same length of the alveolar row of p3-m3; in buccal view, the alveolar row of p3-m3 appears straight along most of the length; dorsal surface of the mandibular body convex with a distinctive swelling below p3-p4; root end of lower incisor reaching the posterior part of p3; large, anterobucally directed mental foramen placed in the buccal side beneath the p3; area below mental foramen and p3 richly fenestrated; masseteric fossa large compared to the size of the jaw.

i1 (Fig. 3.21, 3.22).—Quadrangular, markedly shortened anteroposteriorly; enamel uniformely thick on the anterior part.

p3 (Figs. 2.8 [in part], 3.1–3.5, 3.6 [in part], 3.7–3.13).—Elongated tooth; adult specimens show A1/PR3 pattern stable along the entire tooth crown; one juvenile tooth shows A1/PR4 pattern in the occlusal surface evolving in A1/PR3 in radical side (cf. Averianov and Tesakov, 1997, p. 152). Depth of anteroflexid variable from 6% to 21% of L (average = 14%; N = 14). The anteroconid length ranges from 24% to 31% of L (average = 28%; N = 14); the labial anteroconid tends to be anteriorly more prominent, symmetrical and slightly larger than the lingual one. Protoflexid simple and quite wide, roughly right-angled in most cases; its depth varies from 12% to 21% of W (average = 15%; N = 14). A shallow paraflexid or concavity is present in 86% of specimens, and in two cases the notch is

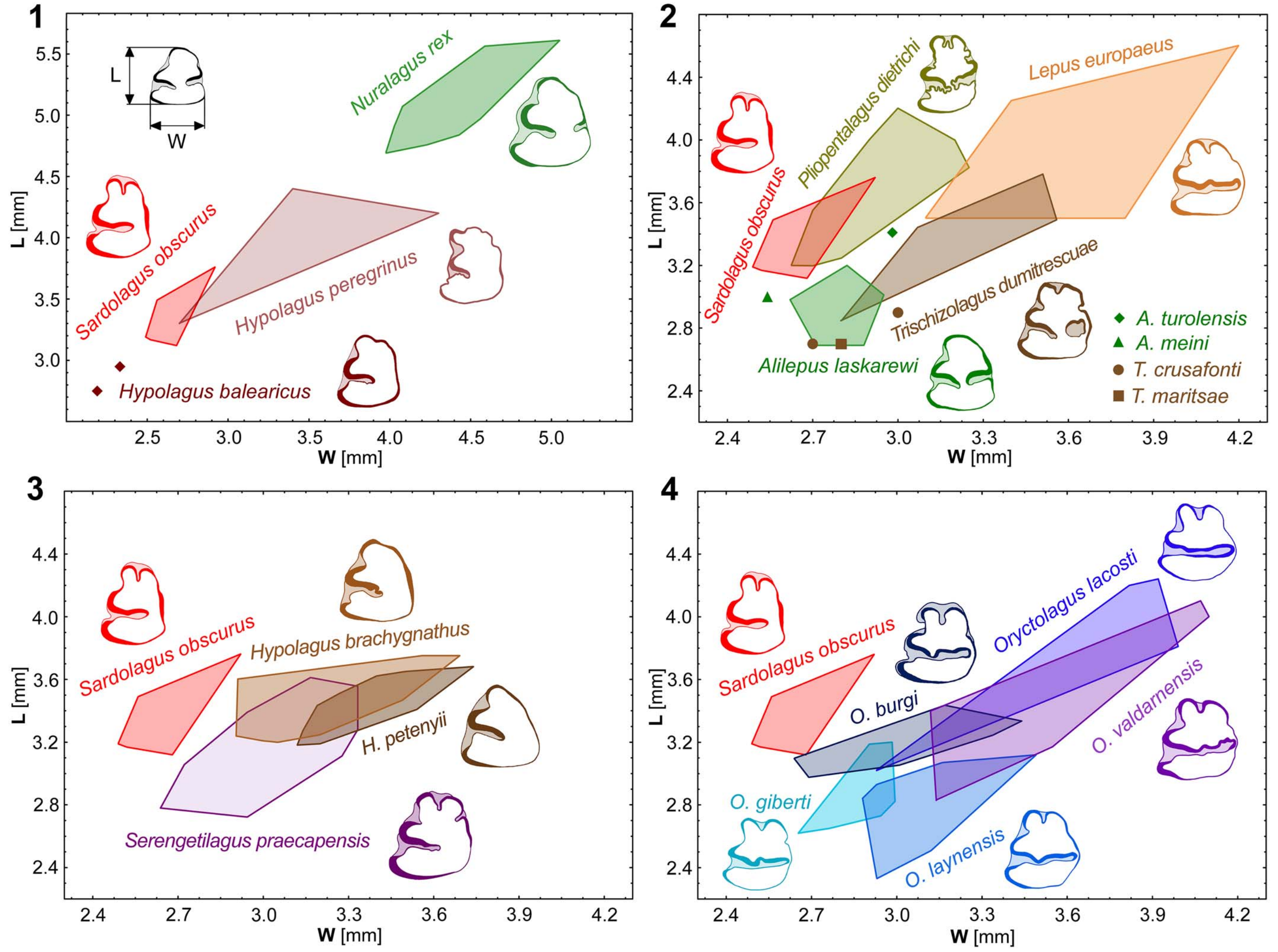

**Figure 5.** Comparison of p3 size and L/W ratio of *Sardolagus obscurus* n. gen. n. sp. with those in (**1**) insular endemic leporids of Western Mediterranean islands and (**2–4**) selected continental Old World species of *Hypolagus*, *Serengetilagus*, *Alilepus*, *Pliopentalagus*, *Trischizolagus*, *Oryctolagus*, and *Lepus*. L = length, W = width.

filled with cement. Hypoconid and protoconid are massive. The hypoflexid is not crenulated, substantially perpendicular to the anteroposterior axis of the tooth, and shallow if compared to other taxa with A1/PR3 pattern of p3, as it ranges from 73% to 90% of W (average = 82%; N = 14). Extremely feeble or absent hypoflexid anterior tip; the hypoflexid lingual end is simple with gradual transition from thick to thin enamel. Labial tip of the hypoconid simple, usually deformed by a shallow notch (in 71% of morphotype “c” [sensu Fladerer, 1987], N = 14).

Lower molariforms (Figs. 2.8 [in part], 3.6 [in part]).—Bulky trigonid with smooth anterobuccal corner (no flexid present); labial part of the talonid frequently deformed by a shallow notch and showing smooth enamel band on the anterior wall; isthmus between trigonid and talonid thin, straight, and short; flexid between trigonid and talonid straight, perpendicular to the anteroposterior axis of the tooth, except for its lingual end (anteriorly curved). Very thick enamel on the labial part of the tooth and on the trigonid posterior edge.

m3 (Fig. 3.23–3.25).—Bean-shaped trigonid, larger and wider than the oval talonid. Enamel thicker on labial edges.

*Etymology*.—After its obscure origin and phylogenetic position.

*Material included*.—(catalog number prefix DSG/URT-053/). **X4**: one fragment of right maxilla, 492; one right I1, 487; two right P2, 428, 429; three left P2, 425–427; 11 right upper molariforms (P4/M1/M2), 445–455; 15 left upper molariforms (P4/M1/M2), 430–444; two fragments of left hemimandible, 485, 486; four right p3, 418–421; three left p3, 422–424; three right p4, 460–462; four left p4, 459, 463, 466, 473; one right m1, 465; six left m1, 456–458, 464, 467, 470; four left m2, 468, 469, 471, 472; one right m3, 491; three left m3, 488–490. **IVm**: one right upper molariform, 484; one left hemimandible, 505; four fragments of left hemimandible, 476–478, 481; one rostral part of right hemimandible, 480; one right mandibular ramus, 479; one left i1, 482; two left p3, 474, 475; one left m3, 483; eight distal epiphyses of humerus, 518–524, 531; one femur, 509; one distal epiphysis of femur, 510; two proximal epiphyses of tibia, 516, 517; four distal epiphyses of tibia, 527–530. **VIIbs**: one incomplete cranium with left P2-M3 (paratype), 504; one fragment of right maxilla with P2-P4, 498; three right upper molariforms (P4/M1/M2), 499–501; one left upper

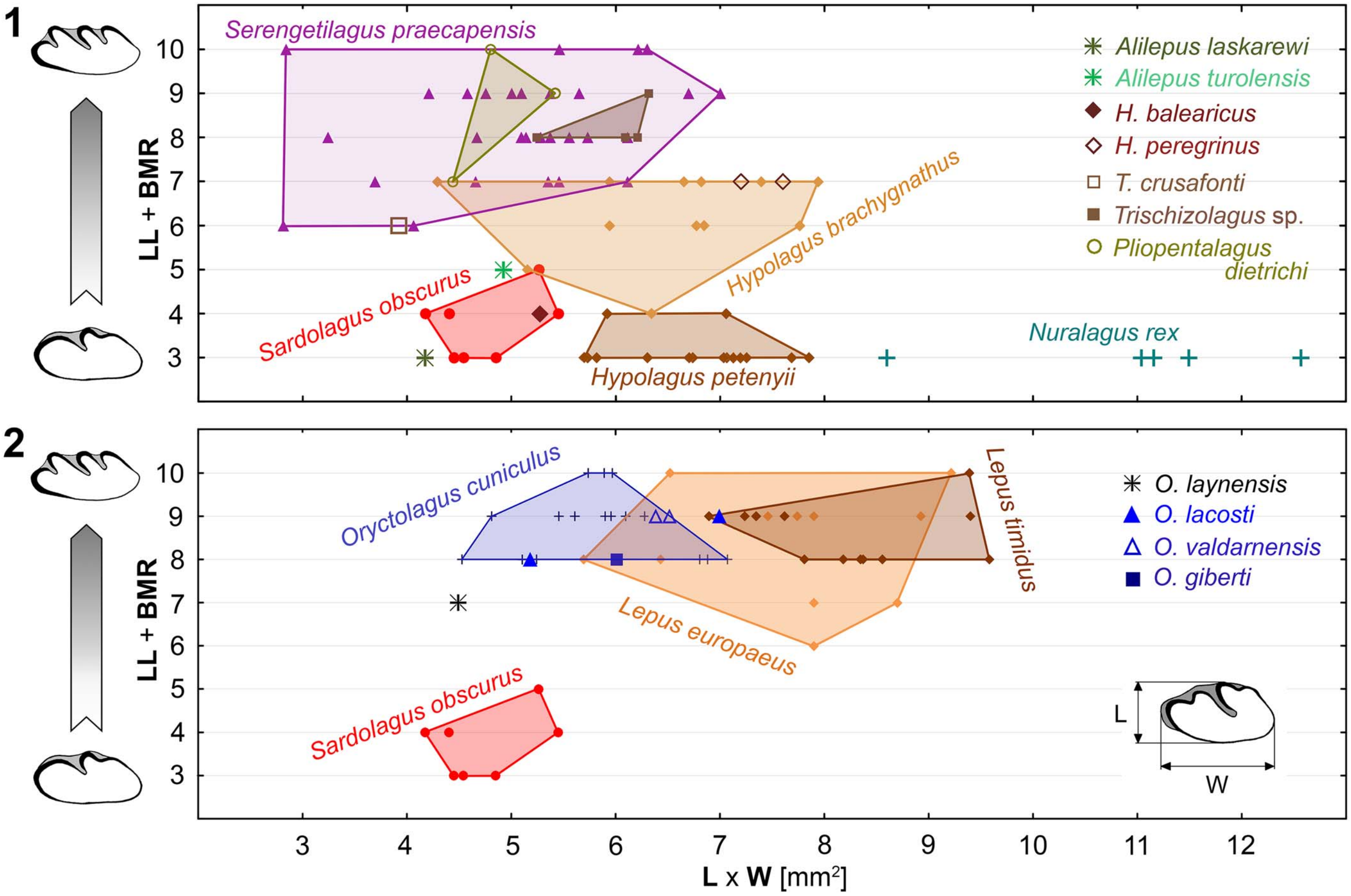

**Figure 6.** Comparison of relationships between occlusal complexity (LL + BMR morphotypes) and size (L multiplied by W) of P2 in *Sadolagus obscurus* n. gen. n. sp. with those in (**1**) selected Old World species of *Hypolagus*, *Serengetilagus*, *Alilepus*, *Pliopentalagus*, *Trischizolagus*, and *Nuralagus* and (**2**) recent species *Lepus europaeus*, *L. timidus*, and *Oryctolagus cuniculus* (including fossil species of the genus). L = length, LL = lingual lobe, BMR = buccal mesial reentrant, W = width.

molariform (P4/M1/M2), 502; one left incomplete hemimandible with p3-m3 (holotype), 503 ; two left p3, 494, 495; one left p4, 496; one left m2, 497; two distal epiphyses of humerus, 525, 526; three distal epiphyses of femur, 506–508; three proximal epiphyses of tibia, 511, 512, 515; two distal epiphyses of tibia, 513, 514.

*Remarks on morphology*.—The extremely flattened incisors are a character unique to the *Sardolagus* n. gen. The incisor "radical" pocket, that in *Sardolagus* n. gen. reaches the posterior part of p3, is a primitive feature often found in *Hypolagus* Dice, 1917 and *Serengetilagus* Dietrich, 1941. The p3 characters are mainly compatible with advanced leporines with PR3 morphotype (Fig. 5) always bearing advanced P2 (e.g., *Oryctolagus* Lilljeborg, 1874; *Lepus* Linnaeus, 1758) (Fig. 6). Whereas the P2 of *Sardolagus*, lacking deep flexa, is compatible with primitive taxa such as *Alilepus* and *Nuralagus* Quintana et al., 2011, and primitive species of *Hypolagus* (e.g., *H. petenyii* and *H. balearicus*) (Fig. 6). Compared with advanced genera with PR3 morphotype, the p3 hypoflexid of *Sardolagus* is quite short and shows an extremely weak or absent hypoflexid anterior tip. Moreover, with respect to p3 of most leporine genera, *Sardolagus* shows an extreme variability of the anteroflexid depth, shape, and inclination.

*Remarks on p3/P2 dimensions*.—The p3 of *Sardolagus obscurus* n. gen. n. sp. is relatively small among western Mediterranean leporids (i.e., between *Hypolagus balearicus* and *H. peregrinus*) (Fig. 5.1). Among the late Miocene–Pleistocene leporids of continental Europe, the L p3 of *S. obscurus* attains values compatible with those of medium-sized taxa, whereas its W p3 is sensibly lower (Fig. 5.2–5.4). In general, the p3 of *Sardolagus obscurus* n. gen. n. sp. has very elongated overall proportions. Its relatively high L/W p3 ratio is comparable with those in other insular endemic leporids of western Mediterranean islands (i.e., their mean values show a linear relationship) (Fig. 5.1). This may suggest a common trait among these taxa. On the other hand, L/W p3 ratios in leporids of continental Europe are lower (Fig. 5.2–5.4). The only exception is *Pliopentalagus* Gureev and Konkova in Gureev, 1964 (Fig. 5.2), which shows overall p3 proportions similar to *Sardolagus obscurus* n. gen. n. sp.

The P2 of *Sardolagus obscurus* n. gen. n. sp. is relatively small if compared to other leporine genera, similar to small-sized fossil taxa *Hypolagus balearicus* (L x W = 1.69 x 3.12), *Alilepus laskarevi* (L x W = 1.48 x 2.82), *A. turolensis* (L x W = 1.49 x 3.30), *Serengetilagus praecapensis* (x̄ of L x W = 1.65 x 3.05, N = 34/33), and *Pliopentalagus dietrichi* (x̄ of L x W = 1.66 x 2.94, N = 3). The P2 size of *Sardolagus*

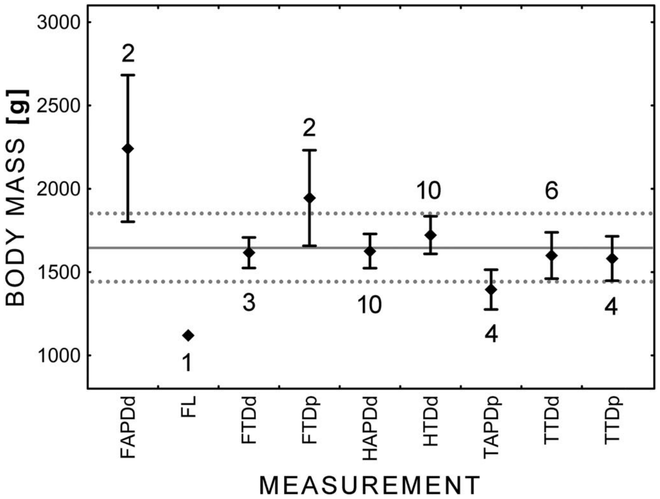

**Figure 7.** Average body mass (= BM, solid gray horizontal line) and interval of confidence (= IC, delimited by dotted gray lines) of *Sardolagus obscurus* n. gen. n. sp. BM estimations (average BM, indicated by the black diamond, and IC, indicated by the vertical solid line) based on different postcranial measurement are reported above each estimator (x axis). The numbers below or above estimations indicate the sample size of each measurement. FAPDd = distal femoral anteroposterior diameter, FL = femur length, FTDd = distal femoral transversal diameter, FTDp = proximal femoral transversal diameter, g = grams, HAPDd = distal humeral anteroposterior diameter, HTDd = distal humeral transversal diameter, TAPDp = proximal tibia anteroposterior diameter, TTDd = distal tibia transversal diameter, TTDp = proximal tibia transversal diameter.

*obscurus* falls in the lower range of extant *Oryctolagus cuniculus* (OR of L x W = 1.57–2.09 x 2.74–3.96, N = 17).

*BM estimation*.—The BM of the Sardinian leporid is estimated ~1650 g (IC = 1443–1856 g; Table 3, Fig. 7). BM estimations extrapolated from measurements performed on tibiae and humeri are quite consistent with this interval, whereas those extrapolated from femora are more erratic. The small sample size (N) of femora (1–3 specimens, depending on the measurement; Table 3) is likely to have biased the results, giving a wider IC. Considering humeri and tibiae, a distal humeral transversal diameter is the measurement that estimated the highest BM. In previous studies of BM estimations of insular leporids, Moncunill-Solé et al. (2015) noticed that in *Nuralagus rex* the distal humeral transversal diameter also overestimated the BM of this species.

## Discussion

*Temporal and geographical distribution of* Sardolagus obscurus.—To date, *Sardolagus obscurus* n. gen. n. sp. has been reported only from a few fissure fillings of the Monte Tuttavista karst complex, thus its distribution seems limited to central eastern Sardinia. This could be due to the extreme scarcity of pre-Middle Pleistocene fossil assemblages in Sardinia and Corsica. However, leporids are unknown even in the well-studied, long-known Capo Figari infillings (see Van der Made, 1999 and references therein), the age of which partly overlaps with the Monte Tuttavista ones.

The material of *Sardolagus obscurus* analyzed in this paper covers the Capo Figari/Orosei 1 FSC of the *Nesogoral* FC and the Orosei 2 FSC of the *Microtus* (*Tyrrhenicola*) FC (e.g., the early Pleistocene) (Fig. 1). Additional material not taken into consideration here (see Abbazzi et al., 2004) is referable to the same FSCs. We lack a quantitative age datum to define the exact age of the fissures. Biochronological considerations based on fossil mammals seem to point out that every single infilling of Monte Tuttavista karst complex was accumulated in a relatively short time span, with a few exceptions (Angelone et al., 2008). This evidence allowed determination of a relative chronological arrangement of the infillings by interpolating the results obtained from several papers mainly centered on single taxa (Palombo, 2009). Single taxa, in fact, may not follow the general trend. For example, according to Palombo (2009), IVm should be younger than X4, whereas preliminary data in Angelone et al. (2009) provide the opposite result (i.e., IVm older than X4, a hypothesis tentatively followed also by Palombo and Rozzi, 2014).

If we follow Palombo (2009), the time span covered by the findings of *Sardolagus* here analyzed is of ~1 Ma (~2.1–1.1 Ma), whereas it is slightly shorter (~1.9–1.1 Ma) if we follow Palombo and Rozzi (2014). If the additional, unpublished leporid remains reported from other Monte Tuttavista infillings (Abbazzi et al., 2004) should pertain to *Sardolagus obscurus* n. gen. n. sp., the youngest record of *S. obscurus* could be at ~0.8 Ma. Similarly, if the undetermined leporid from Capo Mannu D1 (Angelone et al., 2015) could be related to *Sardolagus obscurus* n. gen. n. sp., its first report could be backdated to the earliest late Pliocene (~3.6 Ma) and its known temporal distribution could be extended to western central Sardinia.

*Peculiarities of the dental pattern of* Sardolagus obscurus.—The main evolutionary changes of leporine teeth take place in the anterior parts of their tooth rows, and can be very well observed in the occlusal surface of p3 and/or P2. These changes are formed predominantly by: (1) a selection in tooth structural clusters among the phylogenetic morphoclines leading to a presence of discontinuous p3 patterns (i.e., PR0–4 morphotypes), and (2) a continuous development of morphologies between two morphological states of particular tooth parts (e.g., lengths of flexids/flexa). An effect of the above phenomena on P2 and p3 is generally different, but an overall evolutionary degree of both tooth positions is more or less concordant in the vast majority of leporid taxa.

However, as highlighted in the taxonomic discussion, a significantly discrepant evolutionary degree between p3 and P2 has been observed in *Sardolagus obscurus* n. gen. n. sp. This implies two possible alternative hypotheses: (H1) *Sardolagus obscurus* n. gen. n. sp. developed from an ancestor bearing a primitive dental pattern and maintained a primitive P2 morphotype (LL-II / BMR-A) typical of Archaeolaginae Dice, 1929 and primitive Leporinae, and independently developed a p3 of PR3 type; or (H2) the ancestor of *Sardolagus obscurus* n. gen. n. sp. was a leporine with advanced P2 and p3 morphotypes (e.g., as in *Oryctolagus*), which underwent a selective reverse morphocline that led to the shortening of P2 flexa and of p3 hypoflexid.

In the case of a selective “reversal morphocline” of some characters (hypothesis H2), one may expect in the relatively large sample under study, the occurrence (though in limited percentage) of specimens of *Sardolagus* n. gen. showing the

**Table 1.** Dental measurements (mm) of *Sardolagus obscurus* n. gen. n. sp. CV = coefficient of variation (%), l = width of antero–posteroloph isthmus, L = length, N = number of specimens measured, OR = observed range, W = width, Want = anteroloph width, Wpost = posteroloph width, Wtal = talonid width, Wtrig = trigonid width, x̄ = arithmetic mean.

| Lower teeth | | | | | | Upper teeth | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | N | x̄ | OR | CV | | | N | x̄ | OR | CV |
| **i1** | L | 2 | – | 1.65, 1.79 | – | **I1** | L | 1 | – | 1.69 | – |
| | W | 2 | – | 3.26, 3.46 | – | | W | 1 | – | 3.42 | – |
| **p3** | L | 14 | 3.40 | 3.12–3.76 | 5.35 | **P2** | L | 7 | 1.73 | 1.57–1.83 | 5.38 |
| | W | 14 | 2.68 | 2.49–2.92 | 4.93 | | W | 7 | 2.73 | 2.53–3.01 | 6.34 |
| **p4-m2** | L | 27 | 2.87 | 2.62–3.22 | 5.75 | **P3-M2** | L | 35 | 2.29 | 1.98–2.50 | 5.72 |
| | Wtrig | 27 | 2.75 | 2.41–3.04 | 6.44 | | Want | 35 | 3.34 | 2.85–3.70 | 5.87 |
| | Wtal | 27 | 2.70 | 2.20–3.01 | 7.22 | | Wpost | 35 | 3.58 | 2.65–4.20 | 10.03 |
| **m3** | L | 5 | 1.92 | 1.70–2.15 | 11.15 | | l | 35 | 1.05 | 0.80–1.35 | 13.14 |
| | Wtrig | 5 | 1.76 | 1.60–1.90 | 6.36 | **M3** | L | 1 | – | 0.82 | – |
| | Wtal | 5 | 1.17 | 1.00–1.25 | 8.89 | | W | 1 | – | 1.56 | – |

**Table 2.** Mandibular and cranial measurements (mm) of *Sardolagus obscurus* n. gen. n. sp. CV = coefficient of variation (%), N = number of specimens measured, OR = observed range, x̄ = arithmetic mean.

| | N | x̄ | OR | CV |
|---|---|---|---|---|
| Alveolar length of p3-m3 | 4 | 16.21 | 15.55–16.78 | 3.12 |
| Length of diastema | 6 | 16.02 | 14.68–17.74 | 6.77 |
| Total height of mandible | 1 | – | 34.00 | – |
| Lingual height of mandibular body at p3 | 5 | 11.03 | 10.35–12.28 | 6.87 |
| Lingual height of mandibular body at m3 | 2 | – | 13.28, 14.00 | – |
| Width of mandibular body at p3/p4 | 4 | 5.29 | 4.92–5.54 | 4.97 |
| Width of mandibular body at m2/m3 | 2 | – | 4.79, 4.89 | – |
| Length of mandibular ramus | 3 | 19.06 | 15.51–20.84 | – |
| Width of articular head | 1 | – | 4.08 | – |
| Height of cranium at occipital condyle | 1 | – | 23.58 | – |
| Width of cranium at auditory bulae | 1 | – | 31.95 | – |
| Alveolar length of P2-M3 | 1 | – | 16.03 | – |

hypothetical "original" advanced morphology (see Palacios and López-Martínez, 1980; Averianov and Tesakov, 1997), but this does not occur. This means that the P2 of *Sardolagus obscurus* n. gen. n. sp. shows no trace of the morphology of a hypothetical advanced leporine supposed to be its ancestor. Contrarily, the available P2 phenotype implies an affinity to Archaeolaginae or primitive Leporinae, such as *Hypolagus* or *Alilepus*. The position of the incisor pocket of *Sardolagus* n. gen. reinforces a possible affinity with Archaeolaginae. Such considerations fit with hypothesis (H1).

The presence of morphologically simplified teeth is often explained by paedomorphosis, which is a common evolutionary strategy in lagomorph. The phenomenon is well manifested and described in the extant taxa *Nesolagus* Forsyth-Major, 1899 and *Brachylagus* Miller, 1900 (Averianov et al., 2000). Their dentitions are highly paedomorphic along the entire tooth rows, both upper and lower. In particular, we note a PR4 morphotype of p3 lacking anteroflexid, a reduced P2 with one reentrant, and P3-M2 with very short and simple hypoflexus (see Averianov et al., 2000). In contrast to that, *Sardolagus* n. gen.: (1) exclusively has p3 with "non-paedomorphic" PR3 morphotype; and (2) does not bear any paedomorphic traits of simplification and/or shortening of reentrants in upper and lower teeth.

The relevant question is whether the simple morphology of P2 in *Sardolagus* n. gen. may be explained merely by its small size. In P2, the relationship between size and morphological complexity is very important because genus/species differences are established on the continuous elongation of hypo- and mesoflexus and not on the presence of discontinuous patterns, as mostly in p3 (i.e., PR0–4 morphotypes). Simplified occlusal morphology of P2 with relatively less-developed reentrants is often present in juvenile specimens with a conical tooth shaft where the small-sized simplified occlusal outline differs from the one visible on the root side and disappears during ontogeny (= ontogenetically dependent changes). However, this is not the case for the *Sardolagus* n. gen. material. All analyzed P2s are represented by small-sized prismatic teeth with stable morphology along the entire tooth shaft and belong to adult specimens. So we explored the morpho-dimensional variability and differences among adult P2s pertaining to selected extinct and extant leporid taxa (Fig. 6). The morphology (LL + BMR morphotypes) of prismatic P2 plotted against the tooth size (length multiplied by width) clearly shows that complexity of adult P2 does not depend on size, neither within species nor across species. P2 with a simple pattern increases its size across ancient species in a sequence (from smallest to largest): *Alilepus laskarevi*, *A. turolensis*, *Sardolagus obscurus* n. gen. n. sp., *Hypolagus balearicus* (all four are of comparable P2 size), *H. petenyii*, *Nuralagus rex* (Fig. 6.1). On the other hand, in the comparably small-sized species *Serengetilagus praecapensis* and *Pliopentalagus dietrichi*, the P2 is significantly more advanced (Fig. 6.1). Analyzed recent species *Oryctolagus cuniculus*, *Lepus europaeus*, and *L. timidus* possess comparably advanced P2, but significantly more advanced than in *Sardolagus*; this is also true for all fossil species of *Oryctolagus* (Fig. 6.2). The difference between *Oryctolagus* and *Lepus* is expressed particularly in their P2 size: the P2 of *Oryctolagus* is smaller than in *Lepus*, and dimensionally close to *Sardolagus* n. gen. It is thus evident that in all the analyzed species represented by more abundant material, within intraspecific variability, a degree of P2 complexity is not dependent on its size.

An interesting feature observed in the p3 of *Sardolagus obscurus* n. gen. n. sp. is the lack of the hypoflexid anterior tip, coupled with a relatively shallow hypoflexid. This is quite unusual for a PR3-type leporid, and it is not a secondary detail. It may imply either: (h1) a secondary simplification that follows the above-mentioned paedomorphosis pattern, or (h2) a different genesis for PR3 morphotype in *Sardolagus* n. gen. (i.e., the lingual elongation of a short hypoflexid).

The latter evolutionary hypothesis (h2) about the origin of PR3 pattern in Leporidae has already been formulated by Corbet (1983). In contrast to Hibbard (1963), who hypothesized that the

**Table 3.** Results of body mass estimation (in grams) by postcranial element. IC-L = lower interval of confidence, IC-U = upper interval of confidence, N = number of specimens measured, x̄ = arithmetic mean.

| Bone | Measurement | | N | x̄ | IC-L | IC-U |
|---|---|---|---|---|---|---|
| **Femur** | proximal transversal diameter | FTDp | 2 | 1944.69 | 1657.92 | 2231.46 |
| | distal transversal diameter | FTDd | 3 | 1616.30 | 1524.78 | 1707.82 |
| | distal anteroposterior diameter | FAPDd | 2 | 2241.94 | 1801.88 | 2682.00 |
| | length | FL | 1 | 1119.50 | – | – |
| **Tibia** | proximal anteroposterior diameter | TAPDp | 4 | 1394.86 | 1275.48 | 1514.24 |
| | proximal transversal diameter | TTDp | 4 | 1581.38 | 1447.97 | 1714.80 |
| | distal transversal diameter | TTDd | 6 | 1599.25 | 1460.11 | 1738.38 |
| **Humerus** | distal anteroposterior diameter | HAPDd | 10 | 1626.22 | 1523.30 | 1729.14 |
| | distal transversal diameter | HTDd | 10 | 1722.29 | 1609.39 | 1835.19 |

PR3 pattern of p3 in leporines was derived from PR1 through the morphocline PR1→PR2→PR3 (i.e., *Alilepus*→*Nekrolagus* Hibbard, 1939b → *Lepus* morphotypes; sensu Averianov and Tesakov, 1997), Corbet (1983) regarded as more probable a direct derivation of the PR3 pattern from PR0 (i.e., *Hypolagus* morphotype; sensu Averianov and Tesakov, 1997) by the elongation of a shallow hypoflexid. This conclusion was probably preferred, invoking the parsimony principle, because it requires fewer transformations and is supported by an analogy with p4-m2. Corbet's model was rejected by Averianov and Tesakov (1997). They argued that such a model is not supported by fossil evidence and does not fulfil the parsimony principle because the choice of the hypothesis implying fewer transformations must be done among hypotheses equally supported by facts. We agree that Hibbard´s hypothesis is supported by paleontological evidence, however, in our opinion, the lower probability of Corbet's hypothesis does not exclude its possibility, also because Hibbard's model can not be looked upon as a general phenomenon in all leporine lineages. In fact, Averianov and Tesakov (1997) themselves and Čermák et al. (2015) demonstrated the limited validity of Hibbard's hypothesis. Indeed, it is well documented, particularly in the late Cenozoic North American populations of the lineage *Hypolagus parviplicatus* Dawson, 1958–*Alilepus hibbardi* White, 1991–*Nekrolagus progressus* (Hibbard, 1939a)–*Lepus* ssp./*Sylvilagus* ssp. Averianov and Tesakov (1997) suggested at least two independent parallel developments to explain the origin of the long p3 hypoflexid of advanced leporines: from *Nekrolagus* and from *Trischizolagus* Radulesco and Samson, 1967.

The current fossil record of leporines suggests that the above-mentioned morphodynamic gradients (both continuous and discontinuous ones) took place independently and, most probably, with a different "trigger" (cf., different evolutionary stages of reentrants in *Hypolagus* species limited exclusively to the PR0 p3 morphotype or variable flexa coupled with PR0-PR1-PR2 morphotypes). The length/morphological evolution of p3/P2 reentrants, particularly the anterior ones, seems to be more conditioned by environmental selection pressures than by the basic p3 patterns (PR0–4). Generally, in lagomorphs, the anterior part of tooth row (i.e., P2 and p3) supports a large part of masticatory stress (see the application of Greaves, 1978 schemes to the ochotonid *Prolagus* in Mazza and Zafonte [1987, p. 228, fig. 5], in which p3 is the tooth where the highest muscle resultant is applied). Changes in environmental conditions are steadily and swiftly reflected in these teeth, and because evolutionary pressure should have similar "intensity" in the same part of tooth row, we theoretically expect similar evolutionary degrees in P2 and p3. In fact, fossil and recent species of *Oryctolagus* and *Lepus* possess p3 of PR3/A1 pattern, and concordantly well-developed p3 anteroflexid and P2 hypo-/mesoflexa. The continental endemic extant leporid *Lepus castroviejoi* Palacios, 1977 deserves a special mention; in this species, p3/P2 with advanced morphotypes coexist with p3/P2 with "regressed" characters (Palacios and López Martínez, 1980). However, the concordance seems to be important, at least considering the population in its entirety.

The reason why in *Sardolagus* n. gen. a PR3 p3 with well-developed anteroflexid is coupled with a simple P2 with shallow/absent hypo-/mesoflexa for the moment remains unclear. Such dramatic discrepancy in the evolutionary degrees of p3 and P2 in *Sardolagus* can not be related to insular endemism. In fact, in other western Mediterranean fossil leporids, the concordance of the evolutionary degrees of P2 and p3 is important: (1) in *Nuralagus rex*, the degree of anterior reentrants development in P2/p3 is concordant; in fact in p3 the anteroflexid is missing; in P2 the hypoflexus is missing and the mesoflexus is incipient (it is worth noting, though, that among PR0–PR1/A0 p3, the anteroconid of *N. rex* is relatively advanced [morphotypes III–V sensu Fladerer and Reiner, 1996; see Quintana et al., 2011, fig. 6]); (2) *H. balearicus* has the same (concordance of reentrants development in P2/p3) as in *Nuralagus rex*, however *H. balearicus* dental pattern appears slightly more primitive, showing a PR0/A0 p3 with anteroconid of morphotype III (instead of III–V, as in *N. rex*); and (3) in *H. peregrinus*, the degree of anterior reentrant development in P2/p3 is concordant, but with more advanced, shallow anterior reentrants (Fladerer and Fiore, 2003, fig. 2).

*The BM of* Sardolagus obscurus *in the context of western Mediterranean lagomorphs.*—In insular environments mammals largely undergo Foster's rule: small mammals increase their BM, whereas large ones undergo the opposite destiny (Foster, 1964; Van Valen, 1973). At present, the reasons for these BM shifts have not been fully clarified (see Lomolino et al., 2012). The response of middle-sized mammals as lagomorphs is not as clear as Foster (1964) suggested: extant leporids show a BM shift mostly directed to a reduction of size, but extant ochotonids are not represented in islands and their pattern is unknown (Lawlor, 1982; Lomolino, 1985). Assessing the fossil lagomorphs of western Mediterranean islands, we can shed light on this particular biological trend. Indeed some extinct insular ochotonids of the Mediterranean area appear quite large with respect to continental congeneric taxa (Moncunill et al., 2015, 2016a, b). However, the authors could not undertake direct comparison with the BM of their forebears because, given the present state of the art, they are unknown or their postcranial material is not (well)-preserved. As for insular leporids, they also seem to increase their BM compared to their continental ancestors, but in varying degrees. The western Mediterranean area offers some remarkable case studies. *Nuralagus rex* is considered the largest lagomorph ever with an average BM ~8250 g (see Quintana et al., 2011; Moncunill-Solé et al., 2015), whereas *Hypolagus balearicus* is quite small (BM: ~1300–2700 g, Quintana and Moncunill-Solé, 2014a). The average weight of the species described in this paper, *Sardolagus obscurus* n. gen. n. sp., is ~1650 g (i.e., similar to *H. balearicus* and the two extant insular leporids *Nesolagus netscheri* [Schlegel, 1880] [~1500 g; Sumatra Island] and *Pentalagus furnessi* [Stone, 1900] [~2000–2800 g; Kawauchi, Sumiyo, Amami-Ohshima Island], Yamada and Cervantes, 2005). For the moment, it is not possible to undertake direct comparison with its ancestor (see above and below).

Jointly with changes in BM, insular species endure other biological adaptations (Van der Geer, 2014). Morphologically, insular lagomorphs are characterized by a stiff vertebral column, low sacropelvic angles, and other traits that enable a low gear locomotion (Yamada and Cervantes, 2005; Quintana et al., 2011). Moreover, several investigations have noticed that insular lagomorphs show a life history shift towards the slow end (Yamada and Cervantes, 2005; Riyahi et al., 2011; Köhler et al., 2015; Moncunill-Solé et al., 2016a). The material of *Sardolagus obscurus* n. gen. n. sp. is too poor and we can only make some preliminary inferences about its biology. The allometric analysis evidenced a large distal diameter of the humerus (high humeral epicondylar index). This trait is related with fossorial or burrower lifestyle (digging and scrabbling the ground, or digging holes for habitation) in both rodents (Samuels and van Valkenburgh, 2008) and lagomorphs (Reese et al., 2013). A large distal diameter of the humerus is also substantial in other extinct insular mammals (e.g., *N. rex* and the rodents *Hypnomys morpheus* and *Canariomys bravoi*; see Bover et al., 2010; Quintana et al., 2011; Michaux et al., 2012; Quintana and Moncunill-Solé, 2014b). For the moment, the fossorial or burrower lifestyles of insular dwellers have been interpreted as the requirement of searching for alternative food sources under the low-resource conditions of islands (Köhler, 2010).

It is interesting to highlight that the analysis of teeth size, particularly p3 measurements, is a very common methodology to compare fossil European leporids, due to the abundance of well-preserved dental remains with respect to jaws and postcranials. Such method must be carefully weighted as far as insular endemic lagomorphs are concerned, because of the higher allometric response of dental elements (and especially of the p3) to body size variations with respect to postcranials (Moncunill-Solé et al., 2015, 2016a, b). For this reason, all the procedures of BM estimations of *Sardolagus obscurus* n. gen. n. sp. were carried out with postcranial material.

Sardolagus *in the context of European leporid record*.—The appearance of stem Leporidae in Eurasia is a result of the late Miocene migration(s) from North America via the northern land connection of Beringia (López Martínez, 2008; Flynn et al., 2014). The oldest record appears to be a species of *Alilepus* (Čermák et al., 2015). *Hypolagus* is encountered in Eurasia somewhat later in the fossil record (Čermák, 2009). The relatively rapid spread of leporids across the Old World at ~8 Ma was an important Turolian event and is called the "Leporid Datum" (Flynn et al., 2014). The MN13 record of Leporidae in Europe is relatively rich and available throughout the continent in many localities, but already in the MN12 the record is relatively rare, and limited only to Leporinae. Only a few, very fragmentary findings, undoubtedly indicate the appearance of advanced leporids in Europe before MN12 (Flynn et al., 2014; Čermák et al., 2015). There are also a few, still questionable fossil occurrences suggesting that leporids were present in Europe prior to MN11. Nevertheless, in most cases the relationship of such "early leporid findings" with the accompanying faunal assemblages is not clear or doubtful, making a further evaluation of their age and taxonomy necessary (see Flynn et al., 2014). It is particularly noteworthy that the leporid reports from Sansan (France, MN6, López Martínez, 2012) and Can Poncic (Spain, MN9; López Martínez, 1989) are distinctly anomalous in age. Such occurrences of relatively advanced leporids in the mid-Miocene are not fully compatible with present state of the art on evolution and paleobiogeography of Old World leporids and must be evaluated by future works. At any rate, this record pro tempore, suggests two possible hypotheses (Flynn et al., 2014): (Hh1) in the mid-Miocene of southwestern Europe some archaic lagomorphs could have developed some derived features typical of leporids independently to North American genera; and (Hh2) the "early European leporids" derive from a limited dispersal of leporids into Eurasia prior to the successful late Miocene influx (indeed, advanced leporids could have crossed Beringia before the late Miocene invasion [~8 Ma], leaving only a scattered record.

As for the first hypothesis (Hh1), the relatively rich Miocene record does not support evidence of the independent appearance in Europe of forms with "leporine" characters. The second hypothesis (Hh2) seems the more likely between the two. However, mammalian dispersals from North America into Eurasia were uncommon during Miocene compared to those in the opposite direction (Dawson, 1999), thus the migration of advanced leporids into Eurasia prior to the "*Hipparion* datum" (see Sen, 1989 for details) seems to be extremely improbable. Moreover, the FADs of North American taxa phenotipically matching European ones (see Dawson, 1958, 2008; White, 1988, 1991; Voorhies and Timperley, 1997) do not fit in this model.

The European record of Leporidae, including Archaeolaginae and Leporinae subfamilies, comprises the seven genera listed below accompanied by their FADs in Europe:

*Alilepus*—reliable from MN12 (Čermák et al., 2015);

*Hypolagus*—reliable from MN13 (Averianov, 1996; Čermák, 2009);

*Trischizolagus*—reliable since MN14; the genus has been reported from ?MN13 (with PR0/A1/Pa0 morphotype), however the late Miocene appearance is very poorly recorded and still remains questionable (López Martínez et al., 2007; Čermák and Wagner, 2013);

*Nuralagus*—recorded from the early Pliocene type locality only (Quintana et al., 2011);

*Pliopentalagus*—exclusively limited to MN15, though known also from late MN13 in Eastern Asia (Tomida and Jin, 2009);

*Oryctolagus*—reliable from the early MN16 (López Martínez, 2008);

*Lepus*—reliable from the late MN17 (López Martínez, 2008).

*Arrival of* Sardolagus obscurus *in Sardinia: an open issue.*—Sardinian faunal assemblages were mainly the result of several migrations from the mainland. Early Eocene findings probably are continental endemic taxa whose differences from mainland ones were due to ecological (?filtering) barriers (Kotsakis, 1986, p. 28; reprised in Palombo, 2009, p. 379). Evidence of a late Oligocene migration from the mainland can be recognized in Corsica (Ferrandini et al., 2000), but not in Sardinia, due to the lack of fossil evidence. In Sardinia, the first known migration should have occurred ~20 Ma (MN3), based on the study of the vertebrates from Oschiri (Van der Made, 2008). It must be noted though that the assemblage from Oschiri includes elements of multiple migrations and, very likely, elements that could have been passively transported (e.g., the talpids, De Bruijn and Rümke, 1974) during rotation of the plate. According to Van der Made (2008), the next immigration recorded in Sardinian territory should have occurred ~11 Ma, correlating with a pronounced regression. Other immigrations possibly occurred during the several middle Miocene marine lowstands, however the hiatus in the Sardinian mammalian fossil record between ~20–11 Ma prevents a verification of this possibility (Van der Made, 2008). An earliest late Miocene immigration is recorded by the fossil assemblages referable to the Tusco-Sardinian paleobioprovince, including territories today corresponding to Sardinia and part of Tuscany. The Tusco-Sardinian paleobioprovince remained isolated until the Messinian, apart from some occasional arrivals from the mainland. Several arrivals are recorded in the Baccinello-Cinigiano Basin between 8.3 Ma and 6.7 Ma (Rook et al., 2011; Benvenuti et al., 2015). According to Van der Made (2008), the migrational wave that occurred at ~8 Ma was of particular importance. Because the Tusco-Sardinian PB probably was fragmented in an archipelago (Engesser, 1989), inputs from the mainland did not always reach all the islands, especially the territories corresponding to modern Sardinia (see also Casanovas-Vilar et al., 2011). During the Messinian, Tuscany connected to Italian mainland; in fact, the endemic insular species gave way to continental species, although the region maintained some degree of continental isolation, as demonstrated by the presence of new endemic non-insular species (Angelone and Rook, 2011 and references therein). Sardinia received a wave of continental immigrants during the Messinian and during the early/late Pliocene transition (Angelone and Kotsakis, 2001; Angelone et al., 2015). Later migrations are hypothesized by Palombo (2009) to have occurred during the Piacenzian regressive phase (~2.9 Ma) and at the end of the Gelasian (possibly ~2.1 Ma; extrapolated from Palombo, 2009, p. 369, fig. 2). The first reports of the canid *Cynotherium* at ~1.2 Ma come out in favor of the presence of a landbridge between Sardinia and mainland due to the ecological requirement of carnivorans. Other mammals appear in Sardinia together with or sligthly after *Cynotherium*, reinforcing the evidence of a migrational wave from the mainland. The arrival of *Mammuthus lamarmorai* (Forsyth-Major, 1883), which occurred at the end of the Middle Pleistocene, probably did not require a fully emerged land connection. Indeed, *M. lamarmorai* is the only "foreign" terrestrial taxon that appears in Sardinia in that period (the other new occurrences are lutrins; Palombo and Rozzi, 2014).

Lagomorphs need a landbridge to reach isolated domains (Angelone, 2007). There is no trace of leporids in Sardinia before Leporidae indet. from Capo Mannu D1, however this does not exclude their presence. In the improbable hypothesis that *Sardolagus* n. gen. is related to pre-Turolian leporids, the ~11 Ma regression could be the moment of its immigration. If we relate instead *Sardolagus* n. gen. to modern leporids (which appeared in Europe ~8 Ma; Flynn et al., 2014), we could link the arrival in Sardinia of its ancestor to one of the following.

(1) The major migration episode reported at ~8 Ma (Van der Made, 2008). However, in the Turolian Tusco-Sardinian paleobioprovince, lagomorphs seem completely missing from the Sardinian record (i.e., Fiume Santo; Casanovas-Vilar et al., 2011) and the Tuscanian record is monopolized by *Paludotona*.

(2) The Messinian desiccation of the Mediterranean. It is common opinion that the endemized taxa present in the earliest late Pliocene assemblage of Capo Mannu D1 (the murid *Apodemus mannu* and the glirid *Tyrrhenoglis* aff. *T. figariensis*), could have arrived during the Messinian (Angelone and Kotsakis, 2001 and references therein). In this case, a relationship of *Sardolagus* n. gen. with European continental *Alilepus* (whose record is proven since MN12) or *Hypolagus* (proven since MN13) or a taxon closely related to *Oryctolagus* stock (the first record of *Oryctolagus* is at ~3.5; López Martínez, 2008) could be invoked. A favored migration path could have been through the Italian peninsula, whose Messinian record accounts for some leporids (*Alilepus meini* and the leporid from Brisighella provisionally classified as *Trischizolagus* cf. *maritsae*), which could represent the source of *Sardolagus* n. gen. However, PR1 and PR2 p3 patterns, typical of *Trischizolagus*, are completely lacking in the sample of *Sardolagus* n. gen., thus excluding any close affinity to typical *Trischizolagus*, which also has a more advanced and more variable P2.

(3) The early–late Pliocene regression (~3.6 Ma, age of Capo Mannu D1 assemblage, in which a leporid is recorded). *Sardolagus* n. gen. ancestor could have colonized Sardinia together with the ochotonid *Prolagus sorbinii* Masini, 1989 from mainland Italy (Angelone et al., 2015). The Capo Mannu D1 leporid does not provide any additional weight to this hypothesis, being a sole, broken, non-diagnostic tooth. Nevertheless, though not strictly testable, a direct relationship between Leporidae indet. from Capo Mannu D1 and *Sardolagus* n. gen. is the most parsimonious hypothesis. From the taxonomic perspective discussed above, the most probable continental ancestor in this case should be sought among the earliest forms or an ancestral stock of *Oryctolagus*, whose first appearance should be at ~3.5 Ma (López Martínez, 2008). In this case, the evolutionary scenario would imply a reversal of morphoclines.

Considering the phylogenetic relationship between Leporidae indet. from Capo Mannu D1 and *Sardolagus* n. gen. as the most probable scenario, we consider extremely unlikely the arrival of the ancestor of *Sardolagus* in Sardinia at 2.9 Ma and in all later migration events recorded up to now. Most probably the ancestor of *Sardolagus* n. gen. arrived in Sardinia between ~8 Ma and ~3.6 Ma.

## Conclusions

After a century of paleontological studies, the report of a fossil leporid in the first years of the twenty-first century (Rook et al., 2003) represented a novelty for the vertebrate paleobiodiversity of Sardinia. The remains were provisionally ascribed to the genus *Oryctolagus*. However, our analyses indicated a completely new perspective about its taxonomy, which made the erection of the endemic insular taxon *Sardolagus obscurus* n. gen. n. sp. necessary. The analyzed material was recovered from a few fissure fillings of the Monte Tuttavista karst complex (E Sardinia), referable to the Capo Figari/Orosei 1 FSC and to the Orosei 2 FSC (early Pleistocene, ~2.1–1.1 Ma or ~1.9–1.1 Ma, following either Palombo, 2009, or Palombo and Rozzi, 2014, respectively). Additional leporid remains have been found also in other Monte Tuttavista infillings. If such remains pertain to *Sardolagus obscurus* n. gen. n. sp., following the biochronological schemes proposed by Palombo (2009) and Palombo and Rozzi (2014), the youngest record of *Sardolagus obscurus* n. gen. n. sp. should be at ~0.8 Ma.

A peculiar combination of advanced and primitive features characterizes *Sardolagus obscurus* n. gen. n. sp. A quite primitive P2 lacking deep flexa (predominance of morphotypes LL II and BMR A, after Fladerer and Reiner, 1996) similar to the P2 of *Alilepus* and *Hypolagus*, is coupled with a p3 showing an advanced morphology (PR3 after Čermák et al., 2015) comparable to extant *Lepus* and *Oryctolagus*. The discrepancy in the evolutionary degrees of P2/p3 differentiates *Sardolagus obscurus* n. gen. n. sp. from continental leporids of the Miocene–Pleistocene of Europe and from the other insular endemic leporids of western Mediterranean islands (e.g., *Nuralagus rex*, *Hypolagus balearicus*, *H. peregrinus*), all characterized by a concordant pattern. *Sardolagus obscurus* n. gen. n. sp. differs from other leporids from western Mediterranean islands also by its smaller p3 size, with the exception of *H. balearicus*. An interesting character shared by *Sardolagus obscurus* n. gen. n. sp. and other leporids from western Mediterranean islands, in contrast to continental genera (except for *Pliopentalagus*), is the elongated p3. Unique to the new taxon is the p3 with very variable anteroflexid and unusually, among the PR3 motphotype, short hypoflexid without anterior tip.

The size of p3 is not directly correlated with BM, as highlighted by the study of other insular endemic fossil lagomorphs (Moncunill-Solé et al., 2016b). It is possible to compare the BM of *Sardolagus obscurus* n. gen. n. sp. (average BM: ~1650 g) with other two insular endemic leporids: *N. rex*, which is noticeably larger (Quintana et al., 2005, 2011; Moncunill-Solé et al., 2015), and *H. balearicus*, for which the BM range includes that of *S. obscurus* (Quintana and Moncunill-Solé, 2014a).

The mix of archaic and modern features observed in *Sardolagus obscurus* n. gen. n. sp. may have been attained in two ways: (1) after convergent evolution, which led to an independent origin of PR3 pattern of p3 from an archaeolagine/leporine ancestor bearing a PR0/1 p3; or (2) after a selective reversal morphocline from an *Oryctolagus*-like leporine with advanced P2 and p3 morphotypes. However, given the present state of knowledge, neither hypothesis can be conclusively rejected.

Given the taxonomic framework, it is quite difficult to identify the continental ancestor of *Sardolagus obscurus* n. gen. n. sp. and the moment of its arrival in Sardinia. Crossing the European leporid record and evidence of migrations to Sardinia, we identified three possible moments between ~8 Ma and ~3.6 Ma in which the ancestor of *Sardolagus obscurus* n. gen. n. sp. may have arrived in the Island.

(1) ~8 Ma: Indeed the appearance of modern leporids in Europe marks a biochronological event at ~8 Ma ("Leporid Datum"; Flynn et al., 2014), which is the same age of a major migrational event to the Tusco-Sardinian PB (Van der Made, 2008). In this case, the ancestor for *Sardolagus obscurus* n. gen. n. sp. should be sought among the most ancient "true" leporids of Europe.

(2) Messinian: The arrival of the ancestor of *Sardolagus obscurus* n. gen. n. sp. during the Messinian would imply its relationship to *Alilepus* or *Hypolagus* stock (whose presence in continental Europe is certain since MN12 and MN13, respectively). Unfortunately, there is no trace of leporids in Sardinian assemblages up to Capo Mannu D1 (MN15/M16 boundary, Angelone et al., 2015) to support this hypothesis.

(3) Early/late Pliocene regression: If the absence of leporids up to Capo Mannu D1 is an actual datum and not the consequence of the extreme scantiness of the Sardinian fossil record in pre-Pleistocene times, we may postulate an alternative hypothesis about the arrival in correspondence of the early/late Pliocene regression. In this case, the ancestor of *Sardolagus obscurus* n. gen. n. sp. would be among the earliest forms of *Oryctolagus* and imply a reversal of P2 and p3 morphoclines.

In fact, "true" *Oryctolagus* is known from early MN16 (~3.5 Ma). In this context, the relationship of *Sardolagus obscurus* n. gen. n. sp. with the fragment of a tooth referred to Leporidae indet. collected in Capo Mannu D1 (early/late Pliocene boundary; Angelone et al., 2015) is, for the moment, impossible to unravel. The most parsimonious hypothesis would be an ancestor-descendant relationship.

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