NEW INSIGHTS ON *PALUDOTONA,* AN INSULAR ENDEMIC LAGOMORPH (MAMMALIA) FROM THE TUSCO-SARDINIAN PALAEOBIOPROVINCE (ITALY, TUROLIAN, LATE MIOCENE)

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Abstract. The first vertebrate genus described from the Baccinello-Cinigiano Basin, *Paludotona*, is here revised almost 6 decades after its original description, with the inclusion of new material. *Paludotona* is an endemic insular lagomorph that inhabited the Tusco-Sardinian Palaeobioprovince during the late Miocene (Turolian), in the time span between 8.3–6.7 Ma. The continental ancestor of *Paludotona* remains unknown. We are skeptical about the widely accepted hypothesis of its descent from *Lagopsis*. The retention of archaic dental features in *Paludotona* suggests that its ancestor may have been a pre-MN2 European rooted lagomorph. In our opinion the 'modern' characters observed in *Paludotona* dental elements are the consequence of an evolutionary convergence that was mainly driven by an increased life history triggered by the permanence of an insular environment. We emend the diagnosis of the type species, *Paludotona etruria* from the Baccinello local biochron (mammal assemblage zone) V1, and erect *P. minor* n. sp., from Baccinello local biochron V2. The two species differ in size and several dental characters, and do not form a direct phylogenetic lineage. *Paludotona minor* n. sp. appears to be more closely related to the remains recovered from Baccinello local biochron V0 (referred to *P.* aff. *minor* n. sp.) than to *P. etruria*, which is the temporally closest congeneric species. A few remains referable to the transition of Baccinello local biochrons V1–V2 were ascribed to *P.* cf. *minor* n. sp. These results suggest that the Tusco-Sardinian Palaeobioprovince was fragmented into an archipelago. There is no record of *Paludotona* after the connection of the Tusco-Sardinian Palaeobioprovince and Italian mainland in the Messinian.

INTRODUCTION

Paludotona Dawson, 1959 is a very peculiar endemic lagomorph described from the late Miocene lignite mines in the surroundings of the Baccinello hamlet (Grosseto Province, Italy). The Baccinello lignites were exploited in the early 1950s and are celebrated for having yielded the youngest European Miocene hominoid, *Oreopithecus bambolii* (Hürzeler 1951, 1958; Rook 2016).

The Baccinello *Paludotona* collection curated in the Naturhistorisches Museum Basel (NHMB), derives from a small number of fossil localities in the area of the old Baccinello lignite mine, along the Trasubbie valley (Fig. 1). This study challenges us

(1) to revise the material referred to *Paludotona* originally described by Dawson (1959), (2) to integrate the study of this endemic taxon with the abundant material available almost 60 years after the original description, (3) and to discuss the phylogenetic relationships, as well as the palaeobiogeographic and palaeoenvironmental scenarios in which this peculiar genus lived.

The geology and palaeontology of the Baccinello area are well known thanks to the early researches led by J. Hürzeler from the NHMB, during which abundant faunal remains were recovered from well documented stratigraphic levels (Rook 2016). Since the late 1990s, field campaigns undertaken by the Vertebrate Palaeontology Research Group of the University of Florence, after the initial input of the late Prof. Claudio De Giuli incre-

ased our knowledge of the palaeontology, geology, and sedimentology of the area, providing a better understanding of the sedimentary, environmental and faunal evolution of the Baccinello-Cinigiano (BC) Basin (Rook 2016).

Geological context

The BC Basin is a late Neogene basin located 25 km east of Grosseto in southern Tuscany (Fig. 1). It is one of the largest Tuscan "central basins" sensu Martini & Sagri (1993) and records continental sedimentation throughout the late Tortonian–Messinian. The basin (Fig. 1) is filled with a minimum of 250 m of upper Miocene continental conglomerates, sands, silty clays bearing lignite seams, and freshwater carbonates (Lorenz 1968; Benvenuti et al. 1999a, b, 2001).

Until the first half of the last century, only scattered areas of the BC Basin were the object of concerted research, and these investigations were mainly related to lignite exploitation. The first stratigraphic investigations in the basin began in the late 1950s (De Terra 1956; Lorenz 1968). Lorenz (1968) described its complex lithostratigraphy, which included the occurrence of numerous vertebrate-bearing fossiliferous levels. In recent times this upper Miocene succession has been referred to two unconformity-bounded stratigraphic units (synthems 1–2, Benvenuti et al. 2001; Fig. 1). Synthem 1 (upper Tortonian–lower Messinian) lies unconformably on the pre-Tortonian substratum made of limestone, claystone and sandstone. Synthem 1 is further subdivided into six main units, in some cases with subunits, deposited within different palaeoenvironments ranging from slope-palustrine settings to peat bogs, shallow lakes, alluvial plains, and deltaic-lacustrine settings (Benvenuti et al. 2001). Fine grained deposits in the different units bear relatively abundant fossil mammal remains that are grouped into distinct assemblages (vertebrate assemblages zones V0, V1, V2, and V3; Rook 2016). Mollusc-rich levels characterize specific lacustrine mudstones and limestones, known in literature as F1 and F2 (Gillet et al. 1965; Esu & Girotti 1989; Ligios et al. 2008). Synthem 2 (upper Messinian) rests unconformably on the deposits of Synthem 1 and is stratigraphically overlain by early Pliocene marine deposits ascribed to the *Sphaeroidinellopsis* Zone (Benvenuti et al. 2001, 2015).

Biochronology

The peculiar late Miocene palaeogeographic configuration of emerged lands in the central Mediterranean area gave rise to a specific continental vertebrate palaeobioprovince (Abbazzi et al. 2008b; Rook et al. 1996), whose most complete faunal succession is provided by the geologic record of the BC Basin. Four vertebrate-bearing faunal assemblage zones have been distinguished in Synthem 1 of the BC Basin, referred to as V0, V1, V2, and V3 local biochrons. The faunal assemblages V1 through V3 were established by Lorenz (1968), who arranged different mammal localities with similar faunas into distinct assemblage zones. An older small mammal fauna (described as V0) was discovered some twenty years later in grey marls underlying the V1-bearing sediments (Engesser 1989; Cirilli et al. 2016).

The V0–V2 mammal assemblages

The first three successive BC Basin faunal assemblages (V0, V1, V2) all belong to an endemic faunal complex (OZF, sensu Bernor et al. 2001). The phylogenetic affinities of the mammals of the BC Basin endemic assemblages are shared predominantly with continental European species. Connections with the African biome cannot, however, be ruled out for the ancestry of some taxa, namely some of the artiodactyls, such as the alcelaphine *Maremmia* and the small neotragine *Tyrrhenotragus* (Abbazzi 2008; Hürzeler 1983; Thomas 1984).

The oldest faunal assemblage (V0) includes the murid *Huerzelerimys vireti*, whose occurrence allows a correlation with European sites assigned to the MN11 (early Turolian).

The BC Basin V1 fauna (MN11, early Turolian) occurs in a lignite layer and is considered equivalent to the faunas recovered in coal mines of southern Tuscany (Casteani, Montebamboli and Ribolla; Hürzeler & Engesser 1976). The high level of endemism of the fauna, in conjunction with the low taxonomic diversity, the predominance of specialised bovids, the tendency to the development of hypsodonty, the large body size of some of the rodents, and the absence of non-lutrine carnivores are all indicative of an endemic insular environment (Engesser 1989; Hürzeler & Engesser 1976). The remains of *Paludotona* are extremely abundant in V1.
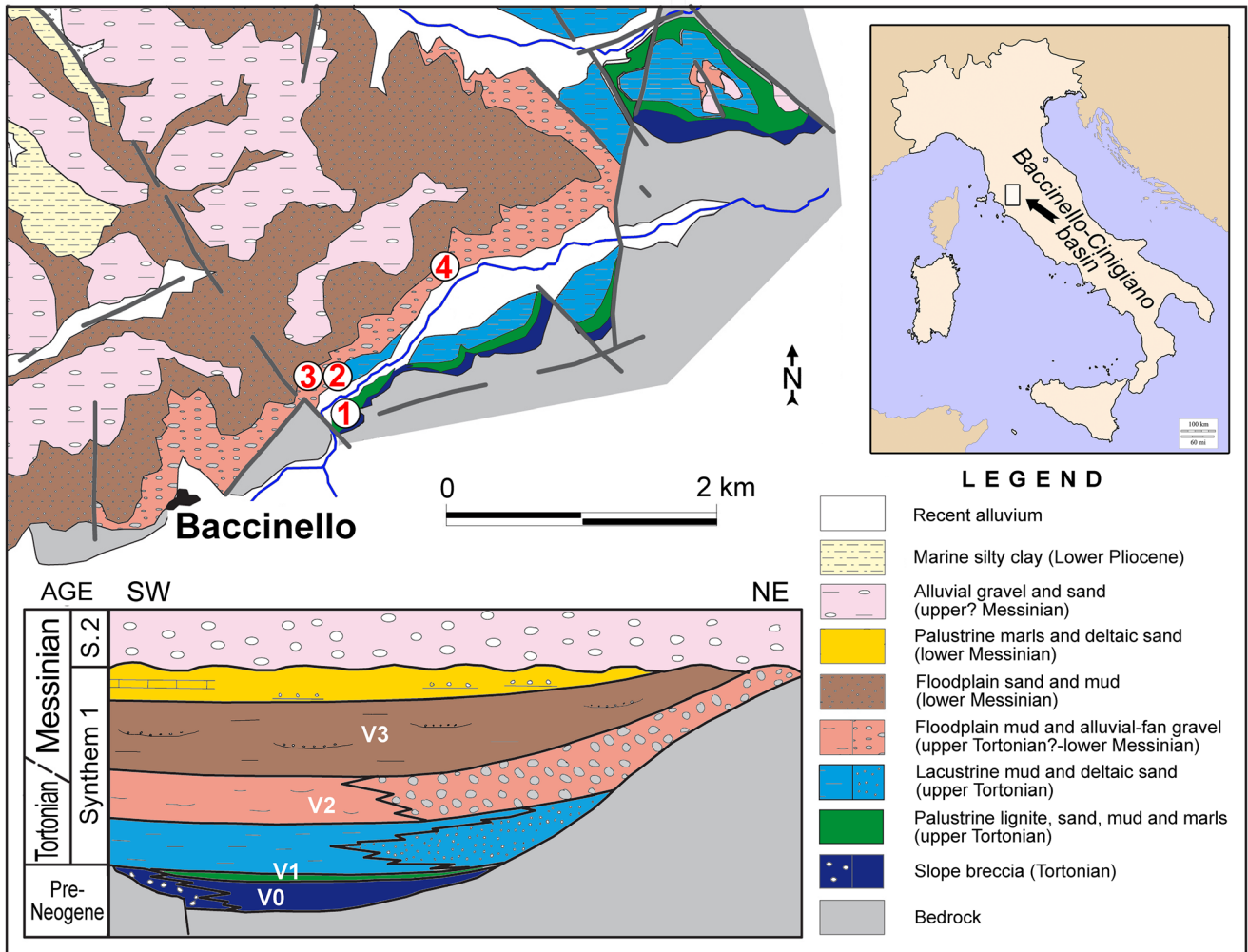
Fig. 1 - Location map with a simplified geologic map of the southern portion of the Baccinello-Cinigiano Basin (BC Basin) and a stratigraphic scheme of the BC Basin succession (modified from Cirilli et al. 2016). Red numbers in white circles indicate *Paludotona*-bearing localities: 1 - Fittaia Creek (Baccinello local biochron V0); 2 - "Über Cardium Horizont" (transition of Baccinello local biochrons V1/V2); 3 - La Pavolona (Baccinello local biochron V2); 4 - Cana 5 (= "Grösser Trasubbie", Baccinello local biochron V2). The material on which the species *Paludotona etruria* was erected, referable to Baccinello local biochron V1, was extracted in the early 1950s during subterraneous mining activities of the lignite seam (whose outcrops are highlighted in green in the map) at a depth of 150-200 m. Thus providing on the map an actual geographical location of the "locality" which bore the remains of *Paludotona etruria* is impossible.

The BC Basin V2 faunal assemblage (MN12, possibly earliest MN13) occurs in fluvial sediments located several tens of meters above the V1 lignite (Benvenuti et al. 2001; Lorenz 1968). Like the earlier V1 fauna, the V2 fauna exhibits a high level of endemism and represents an insular community. However, the V1 and V2 faunas are quite different in their detailed composition and relatively few species are found in both assemblages: *Tyrrhenotragus gracillimus, Anthracoglis marinoi, Paludotona, Oreopithecus bambolii,* and an unidentified species of soricid (Benvenuti et al. 2001; Rook et al. 1996). The key differences between the V1 and V2 faunas arise due to the arrival of new immigrants into the region (i.e., *Parapodemus* sp. II and *Eumaiochoerus*

etruscus, as well as, most probably, *Indarctos anthracitis*), evidence of a temporary reconnection with Europe (Benvenuti et al. 2001). In V2 new species resulting from in situ evolutionary transformation of taxa already endemic of the area can be recognized (i.e., *Anthracomys majori* from *Huezelerimys oreopitheci, Paludolutra campanii* from *Tyrrhenolutra helbingi,* and *Maremmia lorenzi* from *Maremmia haupti*). A quite rich OZF assemblage, correlated with the V2 fauna, is recorded from latest Miocene sediments in northern Sardinia, at Fiume Santo (Abbazzi et al. 2008b; Casanovas-Vilar et al. 2011a, b). *Paludotona* is well represented in V2 assemblages of the BC Basin, but it is completely absent in the Fiume Santo OZF–V2 correlated fauna from Sardinia.

The V3 mammal assemblage

A major reorganisation in the palaeobiogeography of the Tyrrhenian area occurred during the Messinian. From a faunistic (land mammal) point of view, this time interval is characterised by a dramatic change that points to a renewed and definitive palaeobiogeographical connection with Europe. All the taxa belonging to the endemic faunal complex in the BC Basin disappeared, and were replaced by a new faunal assemblage (V3), including continental taxa with clear European affinities. The renewed mammal assemblage V3 is for the most part comparable to typical late Turolian (Messinian) European faunas of MN13 (Rook et al. 2006). This faunal change marks the moment when the Corso-Sardinian massif was definitively isolated from southern Tuscany by the opening of the Tyrrhenian Sea, and southern Tuscany became fully connected with the newly formed Apennine chain. The dispersal of European land mammal fauna throughout the newly emerged lands of the early Italian Peninsula, towards the present-day southern Tuscany, is attested by findings from several localities located along the slopes of the newly emerged Apennines (Abbazzi et al. 2008a; Rook et al. 2006). The latter constituted a wide pathway for the dispersal of mammal communities, although westward, to the structural high point known as the "Mid-Tuscan Ridge", other sedimentary basins still existed, occupied by shallow marine areas with evaporitic deposition (Martini & Sagri 1993).

Chronology (radiometric dating and magnetostratigraphy)

Data suitable for a firmer chronological calibration and stratigraphic correlation come from geochronologic and magnetostratigraphic studies within the stratigraphic succession of the BC Basin (Benvenuti et al. 2015; Rook et al. 2000, 2011). A clear magnetostratigraphy is obtained for the stratigraphic units established in both Synthem 1 and Synthem 2 (Benvenuti et al. 2015; Rook et al. 2011). On the basis of magnetostratigraphic correlation, the stratigraphic record of *Paludotona* in the BC Basin can be summarized as follows:

- the oldest sediments bearing *Paludotona* (V0) are from upper C4r, and so are likely to have an age between 8.3 and 8.1 Ma;

- the youngest *Paludotona* remains (V2) are from sediments attributed to C3Ar, and have an age between 7.1 and 6.7 Ma.

Thus, the maximum chronologic range of *Paludotona* within the BC Basin is about 1.6 Ma, bracketed between 8.3 and 6.7 Ma.

Material and methods

We revised all the material relative to *Paludotona* curated at the NHMB, focusing on the morphology and measurements of I1, cheek teeth, and lower jaws, which were the best preserved elements. We illustrated the occlusal aspect of the teeth using a camera lucida mounted on a Leica binocular microscope. The tooth nomenclature of cusp, occlusal relief, and attritional facets follows Angelone & Hír (2012), Fortelius & Solounias (2000), and Koenigswald et al. (2010). Measurements follow Angelone & Sesé (2009) with the exception of p3 W, replaced by Wtal, a measurement reputed to be more representative in the case of *Paludotona*. All measurement data are given in millimeters. Biostratigraphic terminology for European Neogene Mammal units follows Mein (1999) as revised by Agustí et al. (2001) and updated in Hilgen et al. (2012), whereas local biostratigraphic units follow Lorenz (1968) and later updates (summarized in Rook 2016). All nomenclatural acts presented here conform to the mandatory provisions of the International Code of Zoological Nomenclature (ICZN 1999).

In this paper the family Ochotonidae Thomas, 1897 (including the *Prolagus* clade) is intended without subfamily subdivisions and its representatives are informally called "ochotonids". The informal term "stem lagomorph" is used here for duplicidentates outside of crown group Lagomorpha (= all descendants of the common ancestor of *Ochotona* Link, 1795 and *Lepus* (Linnaeus, 1758) [Asher et al. 2005]). We summarize in the following lines the distinctive characters of ochotonids and stem lagomorphs (relative only to dental features, and extrapolated from López Martínez 2008 and references therein).

Stem lagomorphs are characterized by:
1. relatively low-crowned rooted cheek teeth with a complicated dental pattern bearing persistent folds and cusps;
2. upper cheek teeth, with a peculiar central cusp surrounded by a crescentic, curved valley;
3. upper cheek teeth highly asymmetric, with higher crowns in the lingual side and curving laterally as the lingual root grows more than the labial ones;
4. third molars large compared to Leporidae and Ochotonidae;
5. lower cheek teeth with a conspicuous third lobe (hypoconulid), variable after wear;
6. first lower premolar with small, narrow trigonid and lacking an anteroconid.

Ochotonids are characterized by:
1. P3 persistently non-molariform;
2. enamel of lingual reentrant of upper molariforms not crenulated;
3. shafts of upper cheek teeth more or less curved, extending towards the outer side of the orbit;
4. hypselodonty of upper molariforms attained by a strong torsion of the shafts;
5. tendency to lose M3 and m3 (the latter if present has a reduced or absent talonid);
6. trigonid and talonid of p4–m2 not united by lingual bridge.

Some of the these characters are not mutually exclusive (i.e., do not automatically exclude one taxonomic category in European la-

Paludotona etruria		L	W	Wtal	AA
p3	Bb. 47	3.00			
	Bb. 48	3.13			
	Bb. 50dx	3.35			
	Bb. 50sin	3.48			
	Bb. 51	3.32			
P2	Bb. 43	1.42			
	Bb. 45	1.65			
	Bb. 46	1.26	2.65		
	JH-78*	1.29	2.81		
P3	Bb. 43	2.58			4.00
	JH-78	2.39			3.61
P4	Bb. 43	2.52			4.32
	JH-78	2.32			3.81
M1	Bb. 43	2.68			4.06
	JH-78	2.45			3.68
M2	Bb. 43	2.52			
	JH-78	2.39			3.55
Paludotona minor **n. sp.**		L	W	Wtal	AA
p3	Bac. 806	2.59			
	Bac. 817	2.90		2.77	
	Bac. 818	2.81		3.16	
	Bac. 819	3.12		3.06	
	Bac. 820	2.82		3.03	
	Bac. 827	2.65			
	Bac. 832	3.21		3.06	
P3	Bac. 799a	2.35			4.13
	Bac. 799b	2.29			
	Bac. 801	2.58			3.55
P4	Bac. 799b	2.48			3.35
	Bac. 801	2.58			
M1	Bac. 799b	2.58			3.55
	Bac. 801	2.55			
M2	Bac. 799b	2.65			
Paludotona **cf.** *minor*		L	W	Wtal	AA
p3	Bac. 791	2.90		2.87	
P3	Bac. 780	2.00			2.94
Paludotona **aff.** *minor*		L	W	Wtal	AA
p3	Bac. 1233	2.94		2.97	
P3	Bac. 1234	2.45			3.44
Paludotona **sp.**		L	W	Wtal	AA
P2	JH-63	1.23	2.87		
P3	JH-66	2.48			

Tab. 1 - Tooth measurements (in mm) of *Paludotona* specimens available at present and analyzed in this paper.

gomorphs). There can be cases of ambiguity as for example "*Amphilagus ulmensis*", considered a stem lagomorph by López Martínez (2008), which, however, may have an anteroconid, or "*Amphilagus antiquus*", considered an ochotonid (Lópes Martinez 2008), in which there is no anteroconid, the hypoconulids are evident and persistent and the cheek teeth are relatively low-crowned.

Abbreviations. Dental nomenclature/measurements: AA, partial width; I/i, upper/lower incisive; L, length; M/m, upper/lower molar; P/p, upper/lower premolar; W, width; Wtal, talonid width. Institutions: NHMB, Naturhistorisches Museum Basel. Other abbreviations: BC, Baccinello-Cinigiano; OZF, *Oreopithecus* Zone Faunas.

Systematic Palaeontology

Order **Lagomorpha** Brandt, 1855
Genus *Paludotona* Dawson, 1959
Figs 2, 3; Tab. 1

Original diagnosis (generic and specific): "Dental formula (2)/1, 0/0, 3/2, 2/3. Cheek teeth hypsodont. On P3/ short internal hypostria and J-shaped buccal fold that retains connection to antero-external side of the tooth. On P4/–M2/ only persistent pattern consists of long, straight walled internal hypostria between anteroloph and posteroloph. Posteroloph of M2/ lacks posteriorly directed process. P/3 has shallower anteroexternal and deeper posteroexternal folds and single persistent posterointernal fold. M/3 consists of single column. Coronoid process of lower jaw well developed, lateral in position. Size larger than in *Amphilagus fontannesi*, *Lagopsis verus* and *Ochotona lagreli*." (Dawson 1959: p. 158).

Emended diagnosis: Dental formula 2/1, 0/0, 3/2, 2/3. Very large, rootless, hypsodont teeth. Tooth shaft extremely long, with no torsion and medio-buccal curvature practically absent. p3 with developed anteroconid, three flexids (deep para- and hypoflexid, and shallow protoflexid); the presence, frequency, and development of an additional fold on the lingual part of the anteroconid depends on the species and the age of individuals, being more frequent in juveniles. P2 with only one flexus (paraflexus). P3 with very reduced mesial hypercone, enamel hiatus on mesial hyperloph, multilobed metacone with tridimensional structure. Molarized P4–M2, without fossettes, distal hypercone more protruding lingually than the mesial one; no posterior process on M2. An enamel hiatus is present on the anterior part of the trigonid in lower molariforms. Unilobed m3.

Differential diagnosis: Among ochotonids and stem lagomorphs reported from the Miocene of Europe (see López Martínez 2008) *Paludotona* is the only one with: (1) shaft of cheek teeth very long, with no torsion, and no medio-buccal curvature; (2) P4–M2 with distal hypercone more protrudent than the mesial one.

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. A developed, constant anteroconid united to the trigonid distinguishes *Paludotona* from *Albertona* López Martínez, 1986, *Eurolagus* López Martínez, 1977, *Gymnesicolagus* Mein & Adrover, 1982, *Piezodus* Viret, 1929, *Prolagus* Pomel, 1853, *Ptychoprolagus* Tobien, 1975, *Titanomys* Meyer, 1843, and the species grouped in the genus "*Amphilagus*" Pomel, 1853.

Paludotona etruria Dawson, 1959
Figs 2A-F, 3; Tab. 1

1959 *Paludotona etruria* - Dawson, p. 157, p. 158 (partim).
1976 *Paludotona etruria* - Hürzeler & Engesser, p. 333.
1982 *Paludotona etruria* - Agustí, p. 116.
1984 *Paludotona etruria* - Kotsakis, p. 69.
1986 *Paludotona etruria* - Azzaroli et al., p. 535, tab. 1.
1986 *Paludotona etruria* - Kotsakis, p. 51, tab. III.
1994 *Paludotona etruria* - Palombo, p. 418.
1996 *Paludotona etruria* - Rook et al., p. 4, p. 5, tab. 1.
1997 *Paludotona etruria* - Kotsakis et al., p. 437.
1999 *Paludotona etruria* - Rook et al., p. 194; p. 195, tab. 10.1.
2001 *Paludotona etruria* - Benvenuti et al., p. 101.
2010 *Paludotona etruria* - Van der Geer et al., p. 116.
2011 *Paludotona etruria* - Rook et al., p. 289.
2016 *Paludotona* sp. - Cirilli et al., p. 25.

Dental position	Character	*Paludotona etruria*	*Paludotona minor* n. sp.
p3	size	larger	smaller
	anteroconid shape	robust, roughly symmetrical transversally	flattened, labially elongated
	anteroflexid presence	may occur in juveniles	present in adults (>50%)
	number of attritional facets	2	1 (only anterior)
	connection protoconid-talonid	wide	narrow
	entoconid size and occurrence of hiatus	very large, hiatus variable	large, with constant enamel hiatus
P3	hypercones relative proportions	distal ≈ proximal	distal>>proximal
	mesial hyperloph length	completely covering the metacone	exceeding ¾ of W
	mesoflexus presence	present	not frequent
P4–M2	occurrence and degree hypoflexid crenulation	rare, low degree	frequent, high degree

Tab. 2 - Differential characters between the two species of the genus *Paludotona*.

Holotype: Bb. 43 (Fig. 2E), upper jaw sin with P2–M2 figured in Dawson (1959: p. 160, fig. 2; notice that the figure depicts a composite of Bb. 43 plus an unidentified P2).

Material: Lower jaws sin+dx (Bb. 50, p3–m2 sin + p3–m1 dx); 3 lower jaws dx (Bb. 47, p3–m1+i1; Bb. 51, p3–p4+m2+i1; Bb. 49, p4–m2); lower jaw sin (Bb. 48, p3–m3); upper jaws sin+dx (Bb. 46, P2–M2 sin + P2–M2 dx); 2 upper jaws sin (Bb. 44, P3–M2; JH-78*, P2–M2); 1 upper jaw dx (Bb. 45, P2–M2). *composite.

Occurrence: Fossil site referred to by Dawson (1959) as "Baccinello locality of the 'Grosseto-Lignite'", Tuscany, western central Italy. The lignite seams that in the 1950s yielded the *Paludotona etruria* holotype and hypodigm were exploited in mines and do not outcrop on the surface. At present a lignite outcrop correlated with the main lignite seam (Cirilli et al. 2016) outcrops at the junction of Trasubbie and Fittaia Creeks (="Fosso della Fittaia"; site "1" in Fig. 1).

Distribution: Baccinello V1 local biochron; MN11.

Original diagnosis: Same as genus (Dawson 1959: p. 158).

Emended diagnosis: Very large tooth size. p3 larger than in *P. minor*. p3 with very large, triangular, bulky anteroconid; anteroconid more protruding lingually than the entoconid; two transverse attritional facets are visible on anteroconid and talonid; anteroconid flexid absent in adult individuals; connection trigonid-talonid wide. Lingual enamel hiatus extended and always present on the anteroconid, whereas small and variable on the entoconid.

Differential diagnosis: See Table 2.

Emended description

p3: very large size; very large, triangular, bulky anteroconid; lingual part of the anteroconid more lingually protruding than the entoconid; an enamel hiatus is present on the lingual part of the anteroconid; two transverse attritional facets are visible on anteroconid and talonid; anteroflexid absent in adult individuals; the connection between protoconid and talonid is wide; the entoconid is very large; the presence of a enamel hiatus on the entoconid is highly variable.

Jaws and p4–m2: mandible body extremely thick; cheek tooth shafts extremely long. In upper jaws tooth shafts are very long too. See Dawson (1959) for further details.

P2: very deep paraflexus, directed towards the labial side; a shallow concavity (=hypoflexus?) is frequently present on the lingual side (~75% of specimens).

P3: the wide hypoflexus divides the tooth into two parts of similar length; the distal hypercone is much more protruding than the mesial one; flattened mesial hyperloph, with parallel sides or enlarged at its labial end, with enamel hiatus and completely covering the metacone; quadrangular metacone, with a concavity on the anterior labial part; the main axis of the metacone is perpendicular to the antero-posterior axis of the tooth; the metacone enamel is very thick on the lingual side and shows a three-dimensional, three-lobed structure; in one case a cement lake is present in the metacone (Bb. 43); the paraflexus is very enlarged in its antero-posterior portion.

P4–M2: the hypoflexus is U-shaped and narrow, though it widens at the lingual end, and divides the tooth into two parts of similar length; it approaches the labial end of the tooth in M1–2, whereas it is shorter in P4 (~70% of AA); it is almost straight in P4–M1 and distally curved in M2; a very slight undulation is present at the anterior labial side of the hypoflexus in both M1 and M2 of one maxillary. The distal hypercone is more lingually protruding than the mesial one.

Fig. 2 - Teeth of *Paludotona* from the Turolian of Tuscany (western central Italy). Enamel in black, dentine in white. **A–F** - *Paludotona etruria* from Baccinello local biochron V1: **A** - p3 dx juv. (Bb. 47); **B** - p3 sin (Bb. 48); **C** - p3 sin and p3 dx pertaining to the same individual (Bb. 50); **D** - p3 dx (Bb. 51); **E** - P2–M2 sin (Bb. 43, holotype); **F** - P2–M2 sin (JH-78). **G–O´** - *Paludotona minor* n. sp. from La Pavolona (Baccinello local biochron V2): **G** - p3 sin (Bac. 806); **H** - p3 dx (Bac. 817); **I** - p3 dx (Bac. 819, holotype); **J** - p3 dx (Bac. 820); **K** - p3 dx (Bac. 827); **L** - p3 sin (Bac. 832); **M** - P3–M1 sin (Bac. 801); **N–N´** - lower molariform dx (Bac. 805), respectively occlusal and distal view; **O–O´** - P3–M2 dx (Bac. 799b), respectively occlusal and lingual view. **P** - *Paludotona* cf. *minor* n. sp. from Über Cardium Horizont (transition of Baccinello local biochrons V1/V2), p3 dx (Bac. 791). **Q–R** - *Paludotona* aff. *minor* n. sp. from Fittaia Creek (Baccinello local biochron V0). **Q** - p3 dx (Bac. 1233); **R** - P3 sin (Bac. 1234). **S–U** - *Paludotona* sp. from different localities of Baccinello local biochron V2. **S** - P2 dx, unidentified locality (JH-63); **T** - upper molariform dx, unidentified locality (JH-68); **U** - I1 sin, Cana 5 (Bac. 667).
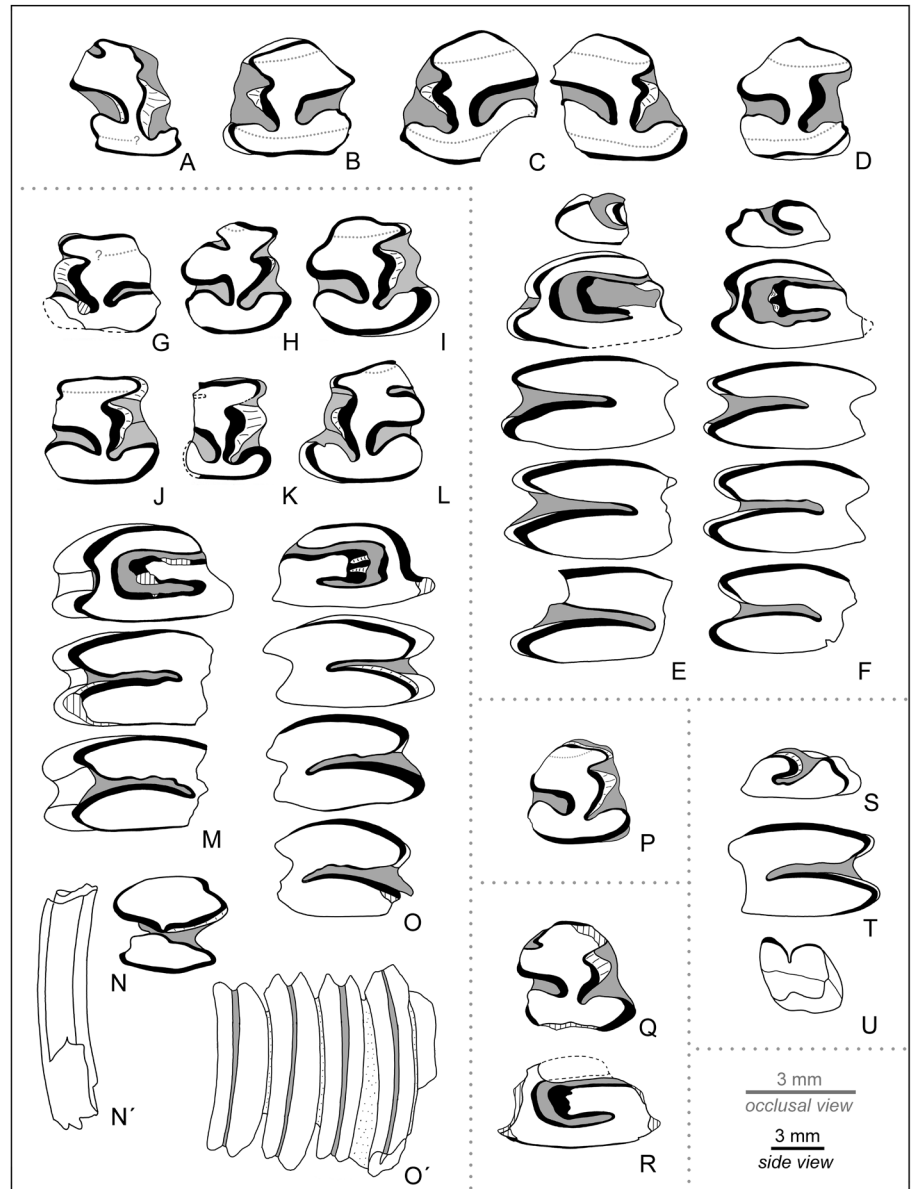
Paludotona minor n. sp.

Figs 2G-O', 3; Tab. 1

1959 *Paludotona etruria* - Dawson, p. 158 (partim).
1976 *Paludotona* aff. *etruria* -Hürzeler & Engesser, p. 334.
1982 *Paludotona* aff. *etruria* - Agustí, p. 116.
1984 *Paludotona etruria* - Kotsakis, p. 69.
1986 *Paludotona* cf. *etruria* -Azzaroli et al., p. 535, tab. 1.
1986 *Paludotona* aff. *etruria* - Kotsakis, p. 52, tab. III.
1994 *Paludotona* aff. *P. etruria* - Palombo, p. 418.
1996 *Paludotona etruria* - Rook et al., p. 4; p. 5, tab. 1 (but *Paludotona* aff. *etruria*); p. 11, tab. 2 (but *Paludotona* aff. *etruria*).
1997 *Paludotona* aff. *P. etruria* - Kotsakis et al., p. 437.
1999 *Paludotona* aff. *etruria* - Rook et al., p. 194; p. 195, tab. 10.1.
2001 *Paludotona* cf. *etruria* - Benvenuti et al., p. 103.
2010 *Paludotona* aff. *etruria* - Van der Geer et al., p. 116.
2011 *Paludotona etruria* - Rook et al., p. 289.

Holotype: p3 dx Bac. 819 (Fig. 2I) from La Pavolona.
Additional material: 3 p3 sin (Bac. 806, Bac. 832, Bac. 818);

3 p3 dx (Bac. 817; Bac. 820, Bac. 827); 4 lower molariforms sin (Bac. 802, Bac. 803, Bac. 810, Bac. 811a); 5 lower molariforms dx (Bac. 805, Bac. 807, Bac. 808, Bac. 823, Bac. 838); 8 I1 (Bac. 799c, Bac. 809, Bac. 812, Bac. 813, Bac. 828, Bac. 829, Bac. 830, Bac. 831); 1 I2 (Bac. 821); 1 P3 sin (Bac. 799a); 2 P3 dx (Bac. 816, Bac. 840); 4 upper molariforms sin (Bac. 800, Bac. 811b, Bac. 798, Bac. 814); 11 upper molariforms dx (Bac. 804, Bac. 815, Bac. 822, Bac. 824, Bac. 833, Bac. 825, Bac. 826, Bac. 834, Bac. 836, Bac. 837, Bac. 839); 1 maxillary fragment sin with P3–M2 (Bac. 801); 1 maxillary fragment dx with P3–M2 (Bac. 799b).

Occurrence: Trasubbie valley, Grosseto (Italy). Site recorded as "La Pavolona" in the NHMB archives (site "3" in Fig. 1).

Distribution: Baccinello V2 local biochron. MN12 (possibly earliest MN13).

Derivatio nominis: Due to its smaller size with respect to *Paludotona etruria*.

Diagnosis: Large tooth size. p3 smaller than in *P. etruria*. p3 with flattened, labially elongated anteroconid; one transverse attritional facet crossing the anterior part of the anteroconid; anteroflexid frequent and of variable depth; posterior part of the protoconid nar-
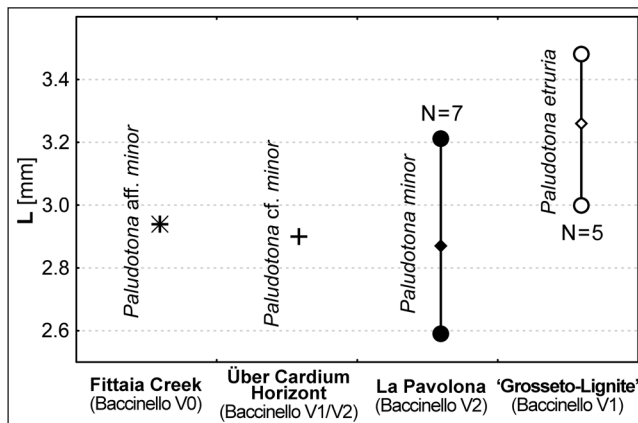
Fig. 3 - Comparison of Lp3 range of *Paludotona* from the Tusco-Sardinian Palaeobioprovince (in mm).

row. Extended enamel hiatus always present on the entoconid, very frequent on the anteroconid. Hypoflexus of P4–M2 often undulated.

Differential diagnosis: See Table 2.

Description

p3: large size; flattened, elongated anteroconid with an undulation on the antero-labial side; one transverse attritional facet is present on the anterior part of the anteroconid; an anteroflexid of variable depth, sometimes filled with cement, is present in more than 50% of adult individuals; the connection protoconid-talonid is narrow. The entoconid is large, with constant enamel hiatus.

p4–m2: the most salient features of these teeth are the enamel hiatus on the anterior part of the trigonids and their occlusal surface that is not flattened but characterized by a high occlusal relief: in the trigonid there can be observed a deep depression of the occlusal surface relative to the attritional surface and a very protruding cusp formed by an enamel blade on the posterior side.

P3: hypoflexus wide to very wide, dividing the tooth into two parts, of which the anterior is noticeably larger than the distal; the distal hypercone is more protruding than the mesial one; the mesial hyperloph is thick, with enamel hiatus on the labial end, going beyond ¾ of the metacone; flattened, quadrangular metacone, in most cases without a concavity on the anterior labial part; the main axis of the metacone is perpendicular to the antero-posterior axis of the tooth; the metacone enamel is very thick on the lingual side and shows a three-dimensional, two- or three-lobed structure; the paraflexus is moderately wide in its antero-posterior portion.

P4–M2: hypoflexus U-shaped and narrow except in its lingual end, dividing the tooth into two parts of similar length; it approaches the labial end of the tooth in M1–2, whereas it is shorter in P4 (~70% of AA); it is straight in P4 and curved in M1–2; it is frequently crenulated on the anterior side and in one case also on the labial part of the distal side. The distal hypercone is more protruding lingually that the mesial one.

Paludotona cf. *minor* n. sp.

Figs 2P, 3; Tab. 1

1994 *Paludotona* aff. *P. etruria* - Palombo, p. 418.
1996 *Paludotona* aff. *etruria* and *Paludotona* sp. 2 - Rook et al., p. 11, tab. 2.
1999 *Paludotona etruria* - Rook et al., p. 194, p. 195, tab. 10.1.

Material: 3 i1 (Bac. 769, Bac. 785, Bac. 786); 1 p3 dx (Bac. 791); 4 lower molariforms sin (Bac. 772, Bac. 773, Bac. 774, Bac. 776); 3 lower molariforms dx (Bac. 770, Bac. 771, Bac. 777); 2 I1 (Bac. 781, Bac. 787); 1 P3 sin (Bac. 782); 1 P3 dx (Bac. 780); 6 upper molariforms sin (Bac. 768, Bac. 775, Bac. 778, Bac. 779, Bac. 783, Bac. 784); 4 upper molariforms dx (Bac. 767, Bac. 788, Bac. 790, Bac. 792).

Occurrence: Trasubbie valley, Grosseto (Italy). Site recorded as "Über *Cardium* Horizont" [= "above the *Cardium* level"] in the NHMB archives (site "2" in Fig. 1).

Distribution: Transition between Baccinello local biochrons V1–V2; MN11.

Description

p3: as in *P. etruria* the connection between protoconid and talonid is wide. However the thin entoconid, and the flattened (though not very elongated) anteroconid with labial protrusion are reminiscent of *P. minor* n. sp., as is the size. Shear facets not observable.

P3: distal hypercone much shorter than mesial one as in *P. minor* n. sp., but size noticeably smaller.

Upper molariforms: hypoflexus not crenulated, as in *P. etruria*, but more stocky in overall appearance as in *P. minor* n. sp.

Paludotona aff. *minor* n. sp.

Figs 2Q-R, 3; Tab. 1

1994 *Paludotona etruria* - Palombo, p. 418.
1996 *Paludotona* cf. *etruria* - Rook et al., p. 5, tab. 1.
1997 *Paludotona* aff. *P. etruria* - Kotsakis et al., p. 437.
1999 *Paludotona* cf. *etruria* - Rook et al., p. 195, tab. 10.1.
2001 *Paludotona* sp. - Benvenuti et al., p. 101.
2016 *Paludotona* cf. *etruria* - Cirilli et al., p. 14, p. 25.

Material: 1 p3 dx (Bac. 1233); 1 P3 sin (Bac. 1234); 1 upper molariform dx (Bac. 1235).

Occurrence: Fittaia Creek, Tuscany, Grosseto (Italy). Site recorded as "Fosso della Fittaia" in the NHMB archives (site "1" in Fig. 1).

Distribution: Baccinello V0 local biochron; MN11.

Description

p3: The sole specimen is large-sized and quite damaged. Flattened anteroconid, broken on the antero-labial side; anteroflexid filled with cement; connection protoconid-talonid not very wide. The entoconid is large and broken in the lingual part.

P3: quite damaged specimen, the wide to very wide hypoflexus divides the tooth into two parts, of which the anterior is noticeably larger than the distal one; the distal hypercone is more protruding than the mesial one; the mesial hyperloph is thick, covering ¾ of the metacone; the enamel hiatus cannot be observed as the distal part of the mesial hyperloph is broken; flattened, quadrangular metacone, no concavity on the anterior labial part; the main axis of the metacone is perpendicular to the antero-posterior axis of the tooth; the metacone is damaged lingually, however it seems to show a three-dimensional bilobed structure; antero-posterior portion of the paraflexus not enlarged.

Paludotona sp.

Fig. 2S-U; Tab. 1

1996 *Paludotona* aff. *etruria* and *Paludotona* sp. 2 - Rook et al., p. 11, tab. 2.

Material: CANA 5: 1 I1 (Bac. 667); 1 upper molariform sin (Bac. 1236); 2 upper molariform dx (Bac. 665, Bac. 666). UNIDENTIFIED LOCALITY: 1 P2 dx (JH-63); 1 P3 sin (JH-64); 1 P3 dx (JH-66); 1 upper molariform sin (JH-67); 2 upper molariforms dx (JH-65, JH-68); i1 dx (JH-77); lower jaw with p4–m1 (JH-26); 4 lower molariforms sin (JH-74, JH-69, JH-70, JH-71); 4 lower molariforms dx (JH-72, JH-73, JH-75, JH-76).

Occurrence: Trasubbie valley, Grosseto (Italy). Site recorded as "Cana 5" (or "Grösser Trasubbie") in the NHMB archives (site "4" in Fig. 1).

Distribution: Baccinello V2 local biochron. MN12 (possibly earliest MN13).

Genus *Paludotona*: taxonomic remarks

The peculiarities of the lagomorph remains from Baccinello V0–2 remarked on above confirm their ascription to a separate genus, *Paludotona*. Our revision of among the available remains identified enough morphological and dimensional differences

(see Fig. 3) to justify the distinction of two species. One of them is *Paludotona etruria* (type species), the other is *Paludotona minor* n. sp. The main differences between the two species are summarized in Table 2.

The Baccinello locality referred to as "Grosseto-Lignite" (local biochron V1) by Dawson (1959) is the type and only locality mentioned for *P. etruria*, whereas La Pavolona (local biochron V2) is the type locality of the new species. Most characters of *Paludotona* from "Über Cardium Horizont" (transition local biochrons V1–V2) may be associated to *P. minor* n. sp., except for the protoconid-talonid connection in p3, which is a taxonomically quite significant character. Such deviation from the standard of *P. minor* n. sp. justifies our ascription of the remains from "Über Cardium Horizont" to *P.* cf. *minor* n. sp.

The main characters of the p3 from Fittaia Creek (local biochron V0) are similar to those of *P. minor* n. sp. from Baccinello V2 (flattened anteroconid, presence of anteroflexid, thinner entoconid, size). Some secondary details, though, do not perfectly fit with *P. minor* n. sp. (protoconid-talonid connection not very wide but not so narrow as in the aforementioned species). The material recovered from Fittaia Creek is extremely scarce and not well preserved, and is separated from the remains of Baccinello V2 by several hundred thousand years. Thus we provisionally refer to such material as *Paludotona* aff. *minor* n. sp.

The scarcity of material and the lack of p3 from Cana 5 (= Grösser Trasubbie) and from an unidentified locality of the Baccinello neighbourhoods (both referable to local biochron V2) do not allow a classification beyond the generic level. The sample from Cana 5 may be referred to *P. minor* n. sp. due to its age (Rook et al. 2011), however we prefer to avoid hasty conclusions and ascribe such material to *Paludotona* sp.

DISCUSSION

Explaining archaic dental features of *Paludotona*

Paludotona retains archaic dental characters (single flexus on P2, persistence of m3, enamel hiatus on lower molariform trigonids, high occlusal relief, three-dimensional structures, and in one case an enamel lake in P3) coupled with advanced features (ever-growing teeth, p3 anteroconid).

A possible explanation for such mix of advanced and archaic features may be paedomorphic phenomena, already observed in insular endemic lagomorphs, as for example the Sardinian anagenetic lineage *Prolagus figaro* López Martínez in López Martínez & Thaler, 1975–*P. sardus* Wagner, 1829 (see Angelone et al. 2015). However they may be excluded in the case of *Paludotona*. Paedomorphy does affect some characters leading to a mosaic appearance, but in paedomorphic populations the occurrence of 'normal' individuals, though rare, is the rule. On the contrary, the quite abundant samples of *Paludotona* are remarkably homogeneous as far as archaic features are concerned. This means that *Paludotona* is a modified archaic lagomorph, which adapted to an insular endemic environment developing some characters that are known to be derived in most lagomorph lineages.

Phylogenetic relationships

Paludotona has been included in the family Ochotonidae since its erection (Dawson 1959) and to the present (e.g., Erbajeva 1988, 1994; Erbajeva et al. 2011, 2015; Dawson 2008; López Martínez 2008). Şen (2003) also follows this taxonomic attribution though remarking that it may be considered a convienient solution, but not possibly the right one ("family Ochotonidae, which I retain here, faute de mieux": p. 164). According to Dawson (1959: p. 164) *Paludotona* could be a "descendant of a line that was near middle Aquitanian representatives of *Titanomys* but in which m3 was retained". This author considered the morphological similarities between *Paludotona* and *Lagopsis* Schlosser, 1884 as due to convergence. However in later papers Dawson referred to *Paludotona* as "a large ochotonid allied to the line of *Lagopsis*" (Dawson 1967), or to *Lagopsis–Paludotona* as one of the two most prominent evolutionary lineages of Europe (Dawson 2008: p. 296). Şen (2003) agreed with the evolutionary line *Marcuinomys* Lavocat, 1951–*Lagopsis–Paludotona*, and so did Marković (2010), Agustí & Antón (2013), and van der Geer et al. (2010). Marković (2010), though noting some characters of *Albertona* fitting with the *Marcuinomys–Lagopsis–Paludotona* line, finally considered their phylogenetic closeness improbable. Bucher (1982) placed *Paludotona* outside of the anagenetic lineage *Marcuinomys–Lagopsis*, and considered *Titanomys* as the sister group of *Palu-*

dotona and *Marcuinomys–Lagopsis*. López Martínez (1986) did not include *Paludotona* in a cladistic analysis that took into account several late Oligocene–middle Miocene genera which the author considered at the time to be ochotonids of the Old World. However in the text *Paludotona* is said to be a descendant of *Lagopsis* which developed in an insular endemic environment, thus confirming the results discussed in a previous paper dealing with the phylogenesis of European ochotonids (López Martínez 1978). This opinion is reported and followed by López Martínez (1989) and Hordijk (2010).

In the taxonomic section we highlighted several features of *Paludotona* that do not perfectly fit with the characters of ochotonids as characterized in Materials and methods. For example the absence of medio-buccal curvature in the upper molariforms is quite peculiar. This absence could be simply a consequence of the increase of the height of the maxilla, and indeed the curvature radius of upper molariforms is quite variable though never tending to zero (cfr. figures in Tobien 1975). Nevertheless this condition, coupled with the lack of torsion of the upper molariform shafts may raise taxonomic questions. In fact, the origin of ochotonid hypselodonty is theorized to have originated in the following way: "ochotonids produce ever-growing cheek teeth by a strong torsion of the shafts, rejecting the buccal roots and cusps towards the exterior of the maxilla" (López Martínez 2008: fig. 4, p. 33). Ochotonids that are not completely hypselodont (i.e., *Piezodus*, see Tobien 1975, figs. 22–30, p. 130–131) may not show shaft torsion in upper molariforms. Moreover, the type of occlusal relief and cusp shape (sensu Fortelius & Solounias 2000) observed in *Paludotona* does not appear the same as in unrooted ochotonids (i.e., *Lagopsis*, in our view erroneously considered a close relative of *Paludotona*), in which the occlusal surface appears quite flat and lacking primitive structures. The overall shape and the retention of archaic structures on the dental occlusal surface of p3 reinforces doubt about the attribution of *Paludotona* to ochotonids sensu López Martínez (2008).

The trigonid-talonid complex in the p3 of *Paludotona* shows an asymmetrical hourglass shape due to the connection/elongation of the protoconid by a lingual cusp (?metaconid). The antero-

conid, present in both species of *Paludotona*, is a feature evolved independently twice in the endemic insular environment of the Tusco-Sardinian Palaeobioprovince, namely in the lineage leading from the unknown ancestor to *P. etruria* and in the lineage leading from the unknown ancestor to *P. minor* n. sp. through *P.* aff. *minor* n. sp. and *P.* cf. *minor* n. sp. The morphology of the anteroconid observed in *Paludotona* is completely different from that of *Lagopsis*, even in primitive species such as *L. spiracensis* Baudelot & Crouzel, 1974 (cfr. the globular anteroconid of *L. spiracensis* vs. the flat anteroconid of *Paludotona*, see Bucher 1982: fig. 8, p. 49 and fig. 10–11, p. 50). The anteroconid of *Paludotona* is also remarkably different from the anterior excrescence, which can be assimilated to an incipient anteroconid, occurring in *Marcuinomys* (see Bucher, 1982: fig. 5–7, p. 47). Other European lagomorphs with hourglass shaped p3 have a symmetrical trigonid (i.e., the genera lumped in "*Amphilagus ulmensis*"; see Angelone 2009) or vary considerably in their morphology during ontogeny (i.e., "*Amphilagus*" spp., see Tobien 1974 for an iconographic overview), whereas *Paludotona* retains a constant hourglass shape throughout its ontogenetic development. As noted by Dawson (1959), the *Paludotona* hourglass trigonid-talonid arrangement is identical to the pattern of some populations included in the genus *Titanomys* (see Tobien 1974: fig. 78, p. 189 and figs. 89–93, p. 198), if we do not take into account the anteroconid, present in *Paludotona* but absent in *Titanomys*. It must be remarked, though, that in addition to the confusion about the genus *Marcuinomys* (see Bucher 1982 and references therein), there is not enough taxonomic clarity about *Titanomys*. The extremely accurate monograph on "*Amphilagus*" and *Titanomys* by Tobien (1974) leads us to suspect that the variability among *Titanomys* remains may override specific boundaries. Some examples:

1. marked differences in p3 ontogenetic development; we note that such differences are one of the main arguments used to distinguish two European rooted lagomorph genera (*Eurolagus* vs. "*Amphilagus*"; López Martínez 1977);

2. presence or loss of roots in upper teeth;

3. presence/absence of m3.

It is evident that a reliable evaluation of the phylogenetic relationships of *Paludotona* cannot be made before a revision of latest Oligocene–early Miocene European rooted lagomorphs. At the present state of the art we can affirm that:

1. the large dental size, the absence of roots, of hypoconulids on lower molariforms, of fossettes and flexa other than hypoflexus in upper molariforms, and the development of an anteroconid on p3 in *Paludotona* are modifications that in our opinion occurred after the arrival of its continental ancestor in an insular domain. The acquisition of these characters is a common evolutionary trend of lagomorphs and is attained independently in several different lineages in different epochs and in different continents. This means that the presence of such characters does not provide any additional clue to assess phylogenetic affinities or temporal constraints for the origin of *Paludotona*;

2. at the present taxonomic state of the art, the p3 trigonid morphology excludes that the closer continental relative of *Paludotona* may be younger than *Titanomys*, as in Europe the last occurrence of a simple hourglass-shaped p3 is observable in *Titanomys*, a genus that has never been recovered in assemblages younger than MN1–2. The presence of m3 in *Paludotona* excludes *Titanomys* from its direct ancestry as in the latter (as we know it today) m3 is reduced or absent and we can not admit the reappearance of a lost dental position;

3. the persistence of archaic structures (see previous section) suggests a considerably phylogenetic distance from European unrooted lagomorphs from MN2 onwards (i.e., *Lagopsis*, *Prolagus*). In particular, the P2 with one flexus is extremely peculiar as it is not known in lagomorphs reported from the European Miocene except for *Alloptox* Dawson, 1961, an Asian genus reported from a couple of middle Miocene localities of eastern and central-eastern Europe (Vasilieadou & Koufos 2005; Angelone & Hír 2012);

4. the similarities between the p3 of *Alloptox* and *Paludotona* are such only at a superficial glance. The p3 of *Alloptox* in all likelihood develops an anteroconid on a basically *Albertona* p3 pattern (i.e., a simple, straight protoconid), and indeed cladistic analyses (López Martínez 1986) confirmed the close relationship between *Alloptox* and *Albertona*, as well as the unexpected proximity of *Alloptox* to the European cluster instead of to the Asian one (nevertheless, see also the latest data from the Valley of Lakes, Mongolia, Erbajeva & Daxner-Höck 2014, in which the appearance of *Alloptox* is shifted back to MN1).

The Tusco-Sardinian archipelago: evidence based on the palaeodistribution of *Paludotona*

The genus *Paludotona* is exclusive to the Turolian of the Tusco-Sardinian Palaeobioprovince. It is represented by different forms in the levels Baccinello V0 (*P.* aff *minor* n. sp.), Baccinello V1 (*P. etruria*), the transition between local biochrons V1 and V2 (*P.* cf. *minor* n. sp.), and Baccinello V2 (*P. minor* n. sp.), but it is worth remarking that it has been recovered only in fossil assemblages located in Tuscany. The remains of *Paludotona gobiensis* of the Mongolian late Miocene (Gureev 1964) are instead referable to *Alloptox gobiensis* (Young, 1932) (see Dawson 1961, 1967; Erbajeva 1981).

The differences between the species of *Paludotona* exclude their direct phylogenetic relationship. The younger species, *P. minor* n. sp., found in Baccinello V2, is smaller and less advanced than *P. etruria* found in stratigraphically older sediments (Baccinello V1). The species found in Baccinello V0 (*P.* aff. *minor* n. sp.) represents the oldest available record of the Tusco-Sardinian Palaeobioprovince). *Paludotona* aff. *minor* n. sp. shows some of the distinctive morphological traits of *P. minor* n. sp., and not a closer resemblance to *P. etruria* as might have been expected due to their similar age. *Paludotona* cf. *minor* n. sp. from the transition V1–V2 resembles *P. minor* n. sp., anticipating its main characters with the exception of the wide protoconid-talonid connection. This latter character is instead shared with *P. etruria*, a fact that can be interpreted as evidence of a common ancestor for the two species. Apparently, modifications of the anterior part have occurred more rapidly than in the rest of the occlusal surface in the evolution of *P. minor* n. sp. Such a window on the evolution of *P. minor* n. sp. is a potential starting point for further studies regarding the modalities, and in particular the sequence of occlusal surface changes during lagomorph evolution. The anteroconids of *P. etruria* and *P. minor* n. sp. are so different that they must have developed independently from a common, not yet recorded, source species in a period of time that predates Baccinello V0. This fact may be explained only with the fragmentation of the Tusco-Sardinian Palaeobioprovince in an archipelago. We are convinced that *Paludotona* did not reach all the islands of the archipelago: its general abundance but complete absence in Fiume Santo (Sardinia; Casanovas-Vilar

et al. 2011a) is likely to indicate a factual absence and not be a consequence of a taphonomic or sampling bias. We exclude an environmental reason to explain the differences among the assemblages of the Tusco-Sardinian Palaeobioprovince. In fact, taxa present together with *Paludotona* in assemblages located in Tuscany are also present in Sardinia, where *Paludotona* is not recorded (see faunal lists in Rook et al. 1996 and updates in Casanovas-Vilar et al. 2011b). Our data:

1. reinforce the hypothesis raised by Casanovas-Vilar et al. (2011b: p. 185) who postulate the existence of a geographical barrier that fragmented the Tusco-Sardinian Palaeobioprovince into two isolated regions, i.e., the Fiume Santo area (Sardinian subdomain) and the Tuscany area (Tuscan subdomain);

2. indicate that the Tuscan subdomain was further fragmented into two or more insular domains, as evidenced by the morpho-dimensional differences between *P. etruria* and *P. minor* n. sp., which categorically exclude their possible anagenetic relationship;

3. exclude that lagomorphs ever reached the Sardinian subdomain.

Engesser (1989) already postulated the fragmentation of the Tusco-Sardinian Palaeobioprovince into different islands based on the occurrence and the intrageneric morphological comparison of murids of the genus *Anthracomys*. In fact, as in the case of *Paludotona* spp., the species of *Anthracomys* present in Baccinello V2 (*A. lorenzi*) could not anagenetically descend from the older species *A. majori* (Baccinello V1 and V2) due to morphological incongruences. Its presence in the BC Basin was considered as the consequence of a migration from a neighbouring island.

The above depicted complex and eventful palaeobiogeographical scenario can be framed in and explained by the intense tectonic activity related to the opening and widening of the northern Tyrrhenian Sea during the latest Miocene (Sartori 2001).

It is not possible to state if the genesis of the two species of *Paludotona* was triggered by the fragmentation of the palaeobioprovince subsequent to the arrival of the ancestor of *Paludotona*, or if it was a consequence of an active colonization of the islands of the palaeoarchipelago, taking advantage of temporary connections due to tectonic/eustatic events.

Age of colonization

The available remains referable to *Paludotona* cover a time-span of ~1.6 Ma (8.3–6.7 Ma). The oldest remains of *Paludotona* are recorded in Baccinello V0 (MN11, i.e., the oldest known age of the Tusco-Sardinian Palaeobioprovince). However, indirect evidence demonstrates that the isolation of the Tusco-Sardinian Palaeobioprovince occurred much earlier. In fact the Baccinello V0 composite assemblage includes species that show variable degrees of modifications related to insular endemism. The modification degree varies from the non-endemic species *Huerzelerimys vireti* which allowed a biochronological correlation with mainland Europe, to highly modified taxa such as *Paludotona* and *Anthracoglis* (Engesser 1989), whose arrival on the island cannot be estimated simply basing on their evolutionary development. Such differences cannot be explained by simply invoking different evolutionary rates (see Angelone & Kotsakis 2001; Furió & Angelone 2010; Angelone et al. 2015 for similar examples in other endemic insular assemblages and detailed explanations). Insular endemic traits develop within a very short time after the arrival of a species on an isolated domain. After that, a slower evolutionary rate, leading to in situ anagenetic evolution, characterizes insular taxa (Island Rule; Mein 1983). New accelerations in evolutionary rate can occur if the equilibrium is modified: a 'restart' of Mein's rule has been observed at the onset of particular conditions in certain western Mediterranean lagomorphs (Moncunill et al. 2016b).

In the case of *Paludotona* the only available temporal constraint derives from dental morphology, which excludes a post MN1–2 continental ancestor. This means that at least 11 Ma separate the arrival of the ancestor of *Paludotona* and the arrival of *Huerzelerimys*. Such a result is congruent with the age estimated for the putative ancestors of the glirids found in the Tusco-Sardinian palaeobioprovince (see Engesser 1983 and Casanovas-Vilar et al. 2011b).

Geographical source of *Paludotona*

The composite assemblage of Baccinello V0 includes species arriving from Europe (*Anthracoglis, Parapodemus*) and others with possible African affinities (*Maremmia, Tyrrhenotragus*). As for *Paludotona*, its morphological dental traits are typically European. In particular we note its p3, which is a variation on the hourglass p3 typical of early European lagomorphs. The p3 of *Alloptox*, a genus widely considered to be of Asian origin, is not to be considered as derived from a hourglass shape, as in our opinion it derives from a previous stage in which the horizontal, anterior part of the trigonid was not yet developed. At the present state of the art, the African fossil record does not include stem lagomorphs, and ochotonids appear in the early Miocene with the genus *Austrolagomys* Stromer, 1926 (López Martínez 2008), which dental morphology is very similar to the Asian genus *Sinolagomys*, with no substantial change with respect to the *Sinolagomys* dental pattern all through the early–middle Miocene.

An emerged connection with Europe was necessary for the ancestor of *Paludotona* to reach the Tusco-Sardinian Palaeobioprovince, given the impossibility for lagomorphs to cross water straits (Angelone 2007). Alternatively, the *Paludotona*-to-be species could have been transported on a terrain that detached from the European mainland. Unfortunately, we lack data about the geodynamic and palaeogeographical characteristics of emerged lands in the northern Tyrrhenian Sea during the latest Oligocene–early Miocene, except for the evidence of the detachment and rotation of the Corso-Sardinian block.

Evolutionary trends in *Paludotona* dental morphology and comparison with other endemic insular mammals

According to Dawson (1967) "the absence of known forms connecting to this genus might suggest its ecological specializations and restriction to a habitat, perhaps forested, not frequently encountered in the Miocene record".

Our hypothetic scenario of the *Paludotona* continental ancestor being a stem lagomorph (i.e., a rooted, probably low crowned taxon), implies radical changes, probably occurred within the insular environment, in a very short time according to Mein's Rule (Mein 1983). With respect to its continental ancestor *Paludotona* achieved:

1. an increase in the masticatory surface (development of p3 anteroconid),

2. the development of a very high crown height, and

3. the attainment of hypselodonty.

The expansion of the masticatory surface by adding the anteroconid 'module' (1) is frequent in

lagomorphs. Improvement of chewing efficiency through addition of modules to basic dental structure is not uncommon among insular endemic mammals, as this strategy was attempted also by the murids of the genus *Mikrotia* (Gargano palaeoarchipelago, Apulia, SE Italy, latest Miocene–?earliest Pliocene; see Maul et al. 2014 and references therein).

Hypsodonty (2) and hypselodonty (3) are customarily related to the need for a more efficient masticatory surface caused by a dietary shift towards hard food and arid palaeoenvironmental contexts. However this is not necessarily true, as lagomorphs with these characteristics have been reported from forested habitats of the European mainland (*Albertona balkanica* López Martínez, 1986; *Alloptox katinkae* Angelone & Hír, 2012). In the case of *Albertona* and *Alloptox katinkae,* such characters and the presence of a thick enamel band (another character that often is uncritically related to the consumption of abrasive food), were explained by invoking a diet based on tough plants and bark.

An increase in hypsodonty can be observed in other Miocene endemic insular lagomorphs of the Mediterranean area. *Prolagus apricenicus* and *P. imperialis* (MN13–?MN14, latest Miocene–?earliest Pliocene Gargano palaeoarchipelago), and *P. figaro* (latest Pliocene/earliest Pleistocene–late early Pleistocene, Sardinia), whose continental ancestors were already hypselodont and provided with an anteroconid. These species increased their masticatory efficiency by developing a higher absolute hypsodonty and a complex, crenulated enamel band (Angelone 2005). *Prolagus sardus* (Middle Pleistocene–historical epoch, Sardinia and Corsica), considered as an anagenetic descendant of *P. figaro*, lost the enamel band complexity (Angelone et al. 2015), but developed an extremely high absolute hypsodonty and the highest hypsodonty ratio recorded in the genus (Angelone 2005: fig. 3, p. 20).

Increased hypsodonty in insular mammals is often explained as a response to aridification (De Giuli et al. 1987 for *Mikrotia*). According to Maul et al. (2014) the dental structure of *Mikrotia* was the response to an increased attrition resulting from a shift to a more abrasive diet. An alternative explanation is an adaptation to an increased food intake (Raia et al. 2003 for dwarfed elephants).

Do we have to postulate that different islands in different epochs all shared the same envi-

ronment? And that insular endemic mammals with different diets, size, and ecological requirements all undergo the same evolutionary pressure? Indeed, insular environments usually share a common characteristic: the available resources are limited. The need to increase feeding efficiency (i.e., through an increase of hypsodonty) may be a response to the high competition in an environment with limited resources.

However, there may be a different explanation: the longevity of insular endemic species, higher than in continental environments due to the different level of extrinsic mortality (see Moncunill et al. 2016a for longevity estimation of insular endemic lagomorph species). A longer life implies a longer use of teeth and makes necessary the development of strategies that combine to preserve tooth efficiency for a longer time span. An increase of tooth crown height is frequent in insular taxa (e.g., the murids of the Sardinian endemic lineage *Rhagapodemus–Rhagamys*, the endemic insular lineages of the murid *Mikrotia* from the Gargano archipelago, and the murids from the Tusco-Sardinian Palaeobioprovince; Angelone et al. 2003; Maul et al. 2014 and references therein; Casanovas-Vilar et al. 2011a). The acquisition of ever-growing teeth, on the other hand, is less frequent, probably because it is less likely to occur or can not be attained in some groups due to evolutionary constraints. The extremely high incidence of teeth worn to the root in *Rhagamys* populations (CA, pers. obs.) attests to a very high degree of wear that could not be fully compensated for, even by a notable degree of hypsodonty. Permanent tooth growth is an evolutionary shift that instead is possible (and frequent) in lagomorphs.

Conclusions

The revision of the original material and of additional remains referred to the lagomorph *Paludotona* Dawson, 1959 collected from several localities referable to Baccinello local biochrons V0–2 led to the following results:

1. the emendation of the generic diagnosis, which has been improved to highlight the peculiarities of *Paludotona* with respect to the European lagomorph genera today included in the family Ochotonidae. In fact, at first glance the tooth morphology of *Paludotona* may recall ochotonids,

and indeed *Paludotona* has been considered as such for almost 60 years. However, with respect to ochotonids as we define them at present, the teeth of *Paludotona* maintain archaic features on the P3 metacone and lack some of the typical characters of ochotonids, such as the enamel hiatus on the trigonid of lower molariforms and the torsion of the shaft and medio-buccal curvature in upper molariforms. All these considerations suggest a closer relationship with stem lagomorphs, a possibility that has to be carefully considered in future studies;

2. the erection of a new species of *Paludotona*; *P. minor* n. sp. The two species of *Paludotona* differ in several characters of the dentition: p3 size, anteroconid shape, presence of an anteroflexid, number of attritional facets, width of protoconid-talonid connection, entoconid size; P3 hypercone proportions, mesial hyperloph length, presence of mesoflexus; degree of crenulation in upper molariforms;

3. the emendation of the diagnosis of *Paludotona etruria*, as the original one coincided with the generic one;

4. the recognition of *P.* aff. *minor* n. sp. found in Fittaia Creek (Baccinello local biochron V0), *P.* cf. *minor* n. sp. from the so-called "Über Cardium Horizont" (transition of Baccinello local biochrons V1–V2), and of *Paludotona* sp. from two localities referable to local biochron V2 (Cana 5 and an unknown locality of the Baccinello neighbourhoods);

5. to highlight the fragmentation of the Tusco-Sardinian Palaeobioprovince in an archipelago. In fact, the morphological cluster represented by *P. minor* n. sp. (V2), *P.* cf. *minor* n. sp. (transition V1–V2), and *P.* aff. *minor* n. sp. (V0) noticeably differs from *P. etruria* (V1). Such differences have a biogeographical value as they indicate that the insular Tusco-Sardinian Palaeobioprovince was fragmented in an archipelago. The fact that *Paludotona* is missing in Sardinian fossil assemblages in spite of its very high relative abundance in all the V0–V2 fossil assemblages of the Tuscanian area strongly reinforces this hypothesis;

6. to propose a pre-MN2 continental European lagomorph with hourglass-shaped p3 as the common ancestor of *Paludotona etruria* and *P. minor* n. sp., thus suggesting a very old age for the dispersal of lagomorphs in the Tusco-Sardinian Palaeobioprovince;

7. to highlight the parallel evolution of the dental morphological characters shared by *P. etruria* and *P. minor* n. sp. We argue that the anteroconid developed independently in *P. etruria* and *P. minor* n. sp., as evidenced by their different morphology and their distinct masticatory assets, indicated by the difference in the p3 shear facets. At the present state of the art we can not state if hypselodonty was attained independently in the two lineages of *Paludotona* or if hypselodont teeth had already been developed by their common ancestor just after isolation;

8. to propose a general explanation for the development of the dental traits customarily associated with the enhancement of masticatory efficiency (i.e., development of anteroconid/anterior modules, hypselodonty, increase of enamel thickness and complexity), which also are traits typical of insular endemic mammals. In our view they must be interpreted as adaptations for an enhancement of masticatory efficiency due to an increased life history, a relevant feature recently highlighted as characteristic of several fossil endemic insular taxa.

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